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Biology and Conservation of Owls of the Northern Hemisphere

Edited by
James R. Duncan
David H. Johnson
Thomas H. Nicholls

February 5-9, 1997
Winnipeg, Manitoba, Canada

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About the Cover: Western Screech-owl (*Otus kennicottii*) wing from the collection of the Slater Museum of Natural History, University of Puget Sound, Tacoma, Washington. The wing was photographed on black velvet by Rollin Geppert. Photo of Great Gray Owl (*Strix nebulosa*) (on binding) by Gerry Jones. Cover layout and design by David H. Johnson with assistance from Lee Telnack and Kris Kirkeby.

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Biology and Conservation of Owls of the Northern Hemisphere

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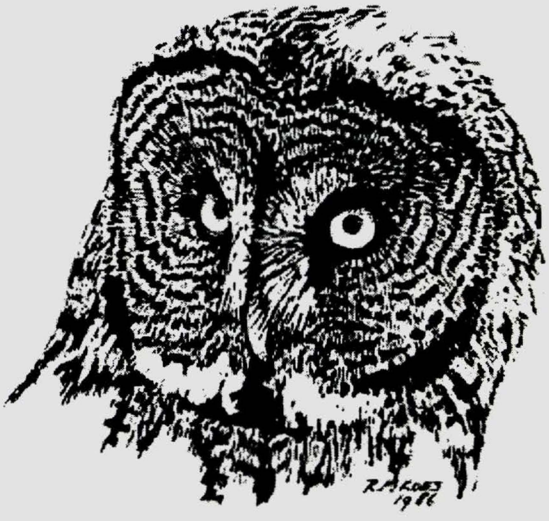
About our Logo:

The Great Gray Owl logo, first used at the 1987 Owl Symposium, is from a sketch by Rudolf Koes.

Rudolf was born and raised in The Netherlands, where he started birding and painting during childhood. He currently teaches in the Winnipeg School Division #1, but spends much of his spare time in the field or working on the forthcoming ***Birds of Manitoba*** book.



Dedication:

This International Symposium on the "Biology and Conservation of Owls of the Northern Hemisphere" is dedicated to the memory of Don G. Follen, Sr.

Don is well remembered for his natural history research on owls, raptors, and other birds in Wisconsin. His active work with the media brought the Great Gray Owl to the attention of thousands. He never lost an opportunity to share his contagious enthusiasm for owls with children and adults from all walks of life.

Don was born 19 August 1939, in the town of Arpin, Wisconsin. He received a degree in Biology from the University of Wisconsin-Stevens Point. Don served in the US Army, was a teacher, and then entered the construction business. In 1986, he founded the still active Wisconsin Foundation of Wildlife Research, serving as its President. A Master Bird Bander, Don received the Don Hasenohrl Award for his dedication and study of birds. The Marshfield Free Library benefited from Don's contribution to its bird collection. He was a member and on the Advisory Board of the Zoological Society of Marshfield, WI. The last day of this symposium marks the ninth year since Don's death at 48 years of age. Many of you will fondly remember Don from the 1987 Owl Symposium.

Don's motivation, his love of owls, and especially his ability to share information encapsulates the spirit of this symposium and sends an important reminder to us all. Sound research and knowledge of owls is not enough to ensure their conservation. Owls and other wildlife, and the habitats that support them, have to be relevant to the public at large. Don's generous efforts helped to make owls important and personal to hundreds, one person at a time.

James R. Duncan

INTRODUCTION

It was the interest and excitement generated by studying Great Gray Owls in Manitoba and adjacent Minnesota that led to the organization of an international symposium on owls of the northern forest in Winnipeg in February 1987. The idea of holding a second owl symposium was first suggested by Jim Duncan, who, with the assistance of his wife Patricia, studied Great Gray Owls, earning a Ph.D. thesis in 1992. Supportive comments by Merlin W. Shoesmith, who played a major role in organizing the 1987 owl symposium, provided strong impetus to hold a second symposium in February 1997, 10 years after the first event. But Denver Holt must also accept some credit for this affair. When Holt informed Duncan in January 1995 that he was planning an owl symposium for 1997 in Missoula, Montana, things began to happen at Winnipeg. What had been a hopeful idea became an action plan almost overnight. Further discussions between Duncan and Holt, and several other owl researchers, led to a decision by mutual agreement to hold a second owl symposium, broadened to include a wider range of species, in Winnipeg. The published proceedings of the 1987 owl symposium describe mainly the technical presentations; the good spirit and fellowship enjoyed by delegates is still a fond memory, and that is part of the reason for wanting to host this second gathering of owl enthusiasts.

Robert W. Nero

PREFACE

Like many of the participants at the 1987 International Owl Symposium, I arrived in Winnipeg for the meeting, took part in the intense discussions and attended the highly entertaining social events and field trips, and then left to resume my field studies. My impressions of the meeting were mirrored in these words of the late Don G. Follen, Sr., from a letter to Bob Nero in August 1987:

"God was that a great experience. I again cannot emphasize the hospitality and professionalism, yet humanism and feeling that was there from around our little globe; simply great."

The 1987 symposium convinced me that there was a need for, and a rewarding career in, owl research. The contagious passion for owls and their conservation was evidently shared by many people from around the world. Owls have significantly altered my life. They have influenced how I make my living, where I live, and most importantly, whom I married. I met Patsy, also a zoologist, while I was studying Great Gray Owls in southeastern Manitoba. Together, we have tried to return the favour, so to speak, back to the owls. In addition to continuing our scientific studies on owls, in 1991 we decided to involve the public in owl research by coordinating a volunteer owl survey in Manitoba. Over 260 people have participated since then.

As 1997 approached, our thoughts more frequently focused on the desire and need for another gathering of the "owl clan". In 1994, I suggested to Bob Nero that we consider organizing a second owl symposium in Winnipeg in 1997. His first recommendation was for me to check with Patsy, now looking after our son Connor and expecting our second child, to see if she would miss me for a couple of years. At the time I did not fully appreciate the effort involved in organizing such an event. Needless to say, Patsy was equally enthusiastic and supportive.

As coordinating chair of the organizing and program committees, I had the pleasure of working with a dedicated crew, including a few seasoned veterans from the 1987 owl symposium. They included: Linda Anderson, Ron Bazin, Robert Berger, Dan Bulloch, Don Campbell, Sherry Dangerfield, Robert Jones, Amy Kearns, Rudolf Koes, Bill Koonz, Tracey Maconachie, Gordon McColm, Glen McMaster, Ted Muir, Robert Nero, Rhonda O'Grady, Margaret Simon, Rosemary Trachsel, and Robert Wheeldon.

In addition to those committee members, the following persons also assisted with the preparations for, and running of this symposium: Robert Arabsky, Garth Ball, Dean Berezanski, François Blouin, Carolyn Curtis, Ward Christianson, Ken Donkersloot, Patsy Duncan, Gene Fortney, Kathy Fox, Maureen Frolick, Gloria Goulet, Judy Grandmont, Herta Gudauskas, Kelly Hamilton, George Holland, Curt Horning, Diane Hupalo, Stavros Iacovides, Koleen Janzen, Gerry Jones, Michelle Kating, Rudolf Koes, Jackie Krindle, Cindy Little, Kurt Mazur, Martine McCall, Robert McCall, Wendy Mendonca, Krista Morrow, Randy Morrow, Ted Muir, Jacques Nadon, Phil Ould, Richard Puttenham, Tanya Rusnak, Brad Safiniuk, Tim Sopuck, Gene Walz, Elizabeth Ward, Elaine Weiss, Gillian Weseen, and Sherry Wurtz.

Some of these people were part of an army of volunteers, coordinated by the indefatigable Sherry Dangerfield, that actually ran the event. The success of the symposium was a result of their hard work. Staff at the Delta Winnipeg Hotel, including Catering Manager Rob Roberts, went beyond the call of duty to assist with the event. Bill Koonz probably put in the longest days, ensuring that all was secure at the end of each day of the meeting. Jim Carson (courtesy of Manitoba Natural Resources), Patricia Duncan and Rudolf Koes kindly permitted the use of their drawings in the program. The Great Gray Owl logo, first used in the 1987 Owl Symposium, is from a sketch by Rudolf Koes.

Rudolf Koes, Bob Jones, and Ron Bazin were instrumental in coordinating and leading the field trips where symposium participants were able to experience an owl phenomenon known as a "winter owl invasion". Gerry Jones, Peter Taylor, and Mel Laurila and family kept us posted on the locations and numbers of owls near Winnipeg to help make final adjustments to the field trip routes. For many, the field trips provided their first view of Great Gray, Northern Hawk, and Snowy Owls, and in numbers which surprised even the most experienced owl biologists!

Since 1987, the Northern Forest Owl Symposium Research Award has been given almost annually to a university graduate student studying owls. In lieu of giving a Research Award in 1997, Bob Nero agreed to award three $150.00 travel assistance grants to the following three symposium delegates: David Arsenault, Reno, Nevada (Mexican Spotted Owl); Paula Enriquez Rocha, Chiapas, Mexico (Tropical Owls); and Randy Lauff, Antigonish, Nova Scotia (Northern Hawk Owl). Other special symposium delegates receiving supporting travel funds provided by the organizing committee included: Heimo Mikkola, Gambia, West Africa; Katherine McKeever, Vineland Station, Ontario; Irina Meyushina, Moscow, Russian Federation; Erkki Korpimäki, Turku, Finland; and David Johnson, Olympia, Washington.

Events such as the owl art exhibit, the owl carving competition and show, and the owl specimen display took place thanks to the energy and talents of many, but were led by Rudolf Koes, Ted Muir, and Richard Puttenham, respectively. Heimo Mikkola, Stuart Houston, Katherine McKeever and Richard Clark provided both entertaining and meaningful addresses at our banquet. Brendan Carruthers and Ted Muir capably served as master of ceremonies for the opening ceremony and banquet, respectively. Finally, thanks are due to all those who came to the meeting, from guest speakers and presenters to artists and registered delegates. Your enthusiasm was the stimulus that kept us all going.

James R. Duncan

EDITORS' COMMENTS AND ACKNOWLEDGMENTS

It has been a privilege to edit these proceedings. The quality of the manuscripts received made this effort enjoyable and educational. We have taken our editorial roles seriously, and while focusing the majority of our energies on the technical and scientific aspects of the manuscripts, we have also been cognizant of the need for readability and consistency. Our editorial task was made much easier due to the efforts of Mary Peterson, Printing Specialist, and Barb Winters, Editorial Assistant, with the USDA Forest Service, North Central Forest Experiment Station, St. Paul, MN. Mary and Tom Nicholls provided authors with clear instructions for the preparation of manuscripts, set up an office at the Owl Symposium and met with almost all the authors, and ensured that work on the proceedings progressed in a timely and professional manner. Each manuscript published in this proceedings was critically peer-reviewed by either one or more reviewers, acknowledged in each paper, with expertise closely aligned to the subject matter. The papers and galley proofs were reviewed by symposium editors for technical accuracy, but the ultimate responsibility for the accuracy of each paper rests with the individual authors. We are also grateful to Bob Nero for checking over the galley proofs of all submitted papers.

Funding to cover the costs of printing the proceedings included the many donors and in-kind contributors listed above. In addition, the following individuals are to be thanked for their pivotal roles in securing financial support from their respective agencies: Erick Campbell, Bureau of Land Management, Portland, OR; Richard Buech, USDA Forest Service, North Central Forest Experiment Station, Research Work Unit NC-4351, Grand Rapids, MN; Kate Benkert and Tim Bodurtha, USDI Fish and Wildlife Service, Oylmpia, WA, and Kalispell, MT, respectively; Geoffrey Holroyd, Canadian Wildlife Service, Environment Canada, Edmonton, Alberta; Stephen Penland, The Wildlife Society-Washington Chapter, Olympia, WA; Caroline Caza, Wildlife Habitat Canada, Ontario, Canada; and Mark Fuller, Raptor Research Center, Boise State University, Boise, ID.

Clearly, much has happened in owl conservation since the 1987 symposium. In the proceedings that resulted from that meeting, Merlin Shoesmith asked the still relevant question "How have ... owls benefited from this symposium?" We would venture that the exchange of ideas and knowledge, renewed commitment, and identification of information gaps will affect owl conservation in a positive way. The opening addresses from Merlin Shoesmith, Brian Gillespie, and Michael Bradstreet provided insight into how owls fit into the ever changing approaches to conservation in general. Clearly, habitat and landscape level approaches to the conservation of the earth's resources represent a coming of age for humankind. But some level of species-specific information is necessary to assure our success. Richard Clark, in his closing remarks, provided us with future direction with a plea for more research on lesser-known owls and studies in parts of the world where information is lacking. Although these proceedings focus on Northern Hemispheric owls, we support owls and owl conservation worldwide and thus have included a paper on an owl species from the Southern Hemisphere. The next International Owl Symposium, wherever and whenever it may be, will be a welcome event celebrating the role of owls in their environments and in our lives.

James R. Duncan
David H. Johnson
Thomas H. Nicholls

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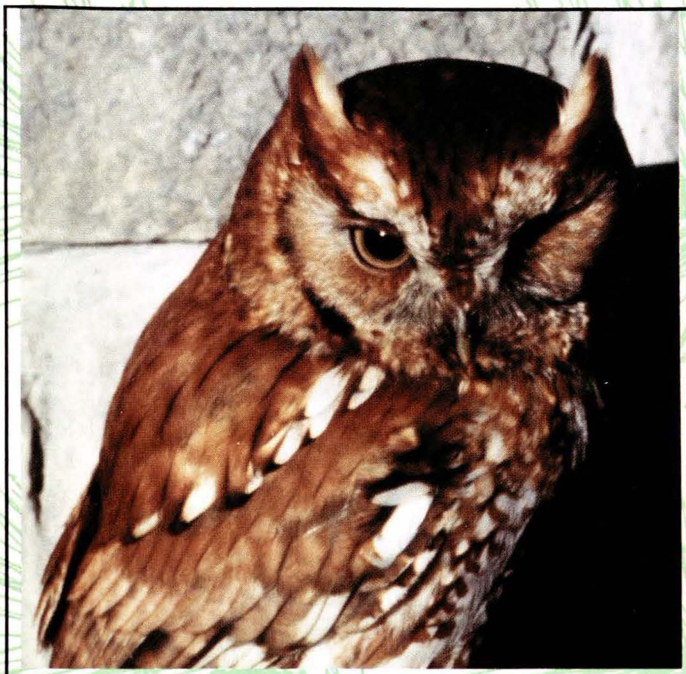
***About the Following Color Section*:** The photographs used in the color section reflect the majority of the owl species for which presentations were made at the symposium. Two photographs of the Northern Saw-whet Owl, Queen Charlotte Island race (*Aegolius acadicus brooksi*) were included, as these are among the first ever published photographs of this owl. We thank all of the photographers who have so graciously submitted their slides for inclusion. Color section layout and design by David H. Johnson.

Barn Owl (*Tyto alba guttata*), Central European race. Burgundy, France. Photo by Philippe Perrot.

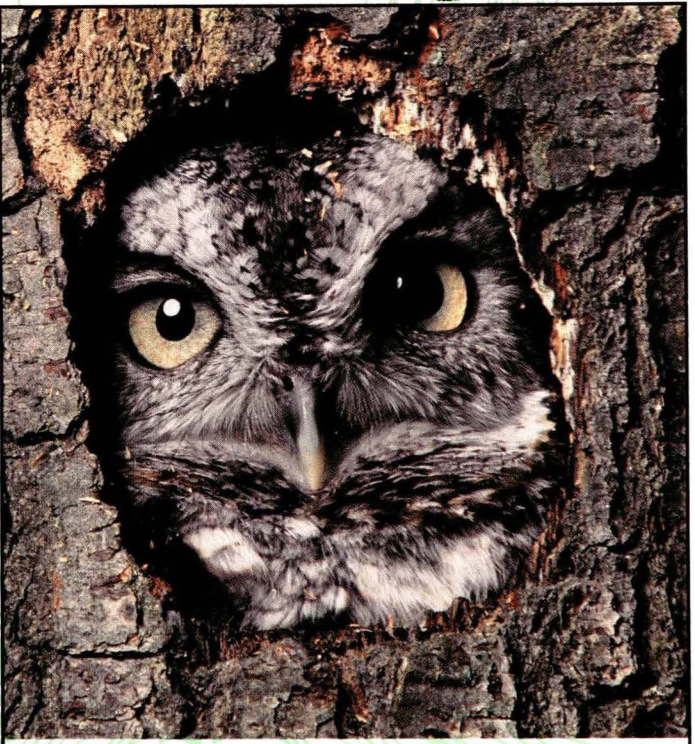
Barn Owl (*Tyto alba alba*), British and South European race. Burgundy, France. Photo by Philippe Perrot.

Barn Owl (*Tyto alba pratincola*), North American race. Photo by Lorraine Andrusiak.

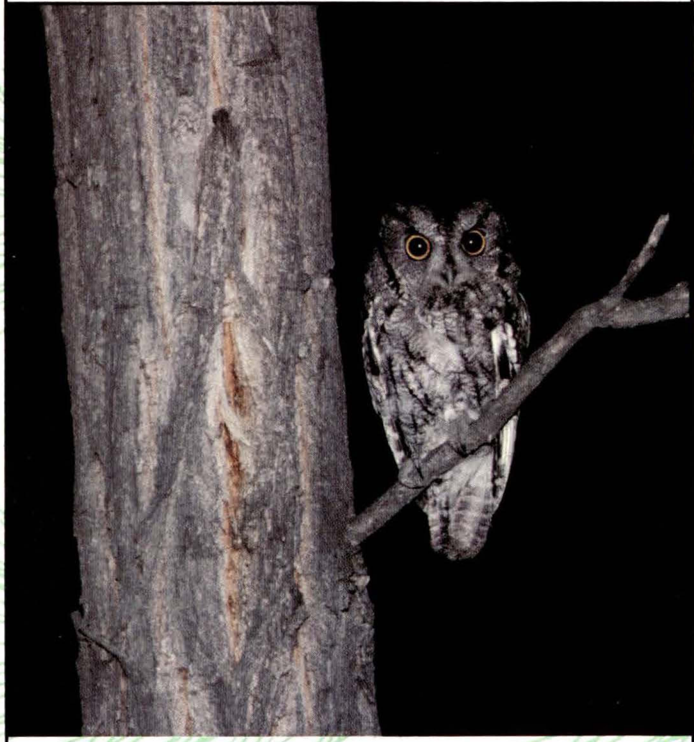
Flammulated Owl (*Otus flammeolus*). Roosting female. Photo by Brian D. Linkhart.



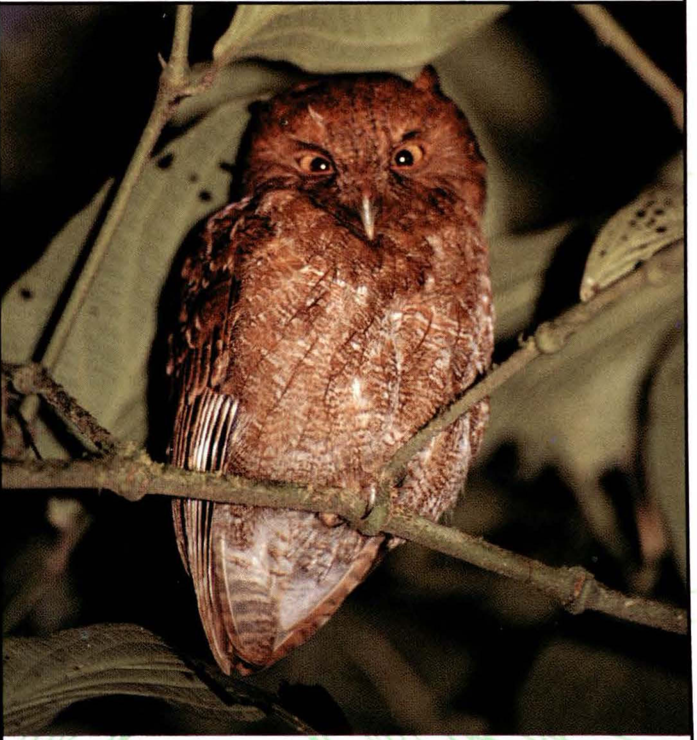
Eastern Screech-owl (Otus asio), rufous morph. Photo compliments of Katherine McKeever, The Owl Foundation.



Eastern Screech-owl (*Otus asio*), gray morph. Photo by Mark Wilson (WILDSHOT, PO 220, Dunstable, MA 01827-0220, USA).



Western Screech-owl (*Otus kennicottii*). Photo in Idaho, USA, by Jim Belthoff.



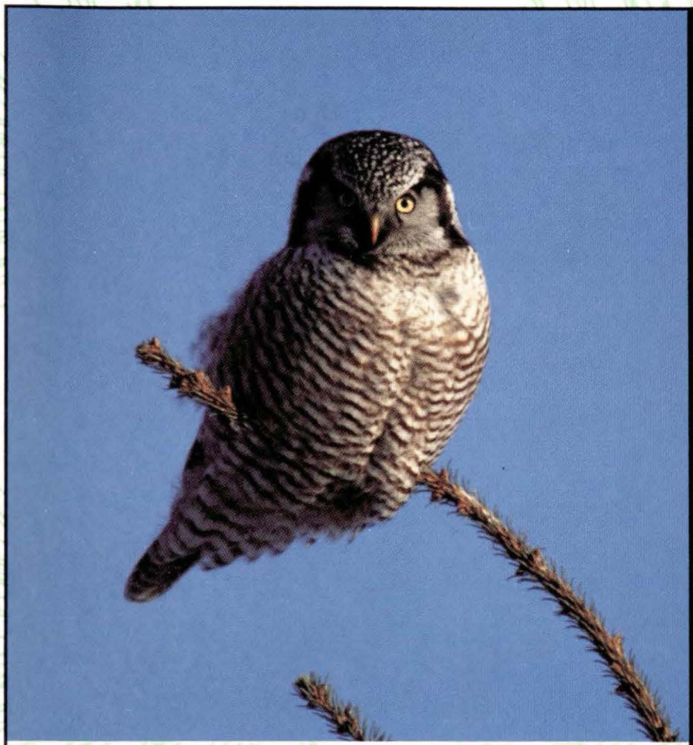
Vermiculated Screech-owl (*Otus guatemalae*). Photo from La Selva Biological Station, Costa Rica, by Jose´ Luis Rangel Salazar.

Crested Owl (*Lophostrix cristata*). Photo from La Selva Biological Station, Costa Rica, by Jose´ Luis Rangel Salazar.

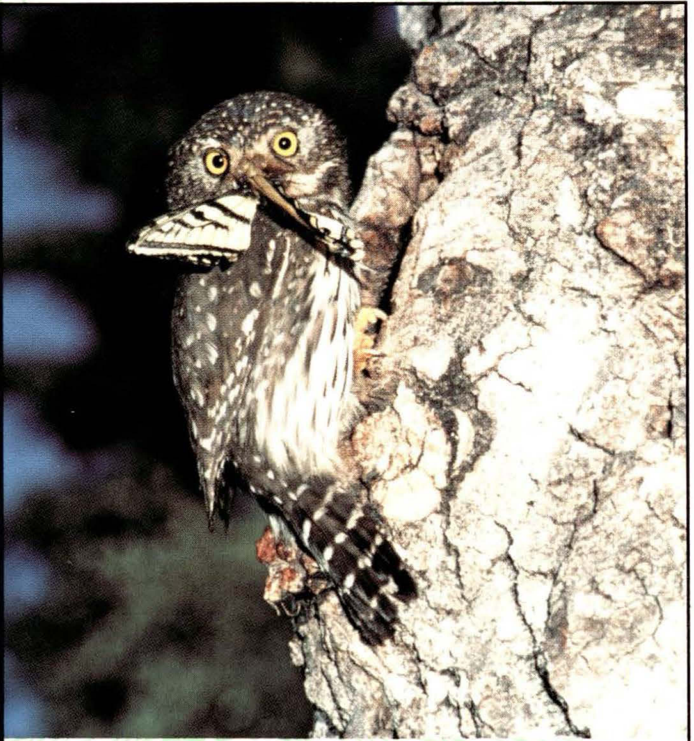
Great Horned Owl (*Bubo virginianus*). Photo by Rollin R. Geppert.

Eurasian Eagle-Owl (*Bubo bubo*). Photo by Doug Ross.

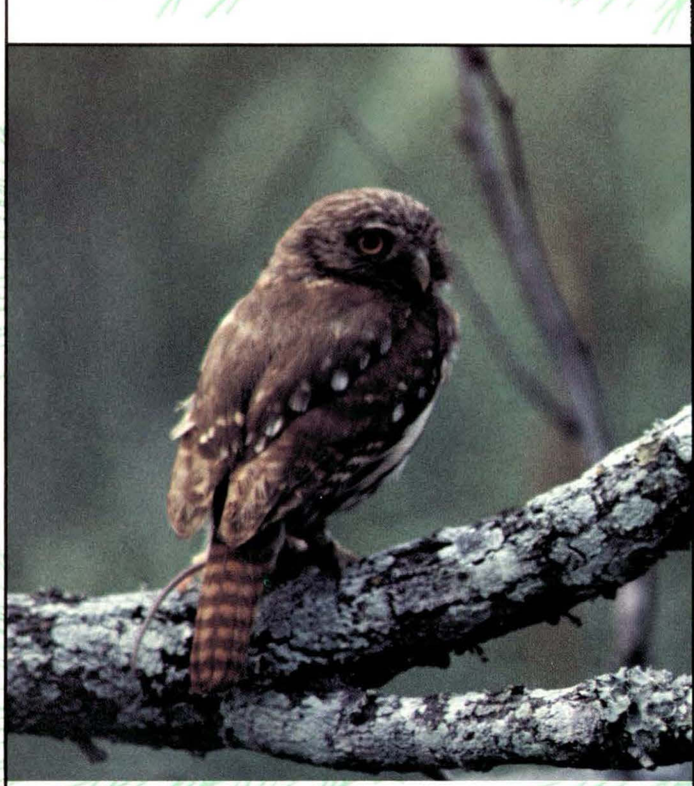
Snowy Owl (*Nyctea scandiaca*). Photo by Mark Wilson (WILDSHOT, PO 220, Dunstable, MA 01827-0220, USA).



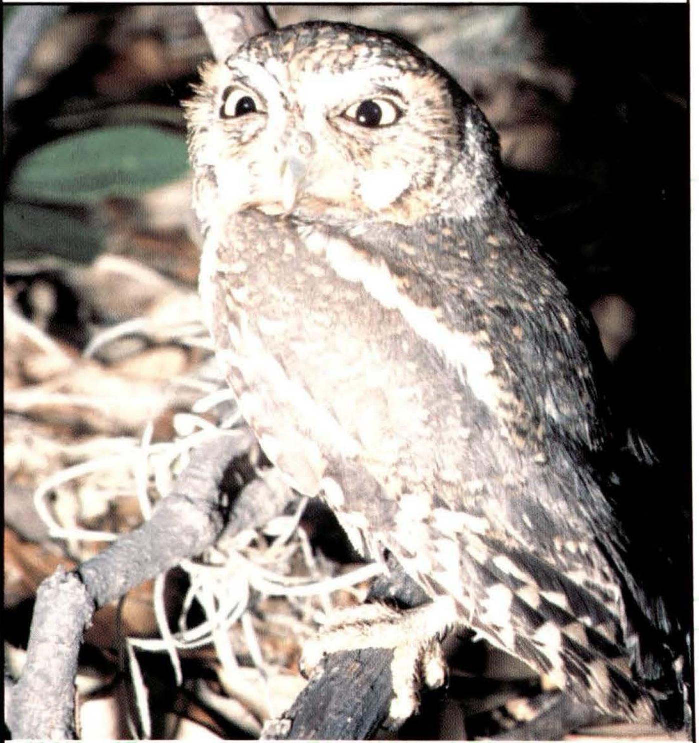
Northern Hawk Owl (*Surnia ulula*). Photo in Manitoba, Canada, by Gerry Jones.



Northern Pygmy-owl (*Glaucidium gnoma*) at nest with Swallowtail Butterfly. Photo by R.E. Gehlert.



Ferruginous Pygmy-owl (*Glaucidium brasilianum*). Photo by Glenn Proudfoot.



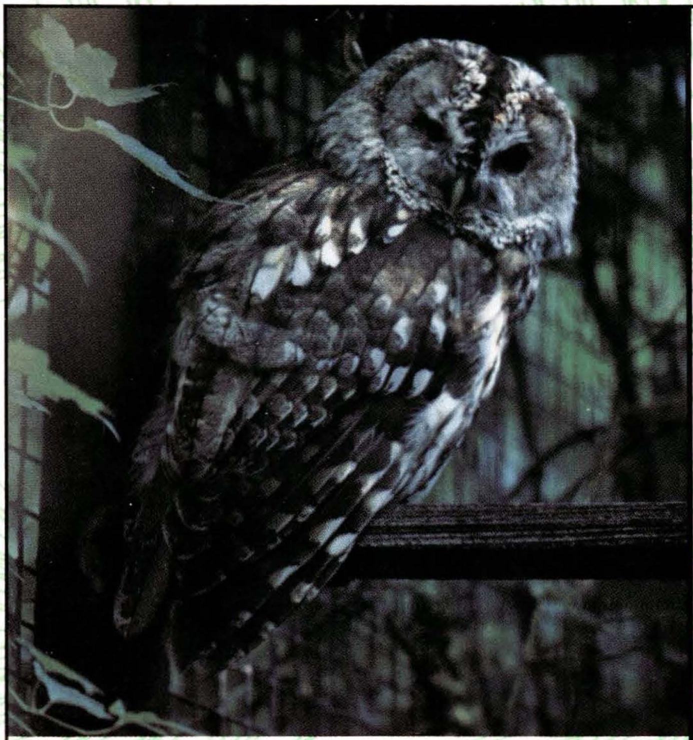
Elf Owl (*Micrathene whitneyi*). Photo by Edgar T. Jones.

Burrowing Owl (*Athene cunicularia floridana*), Florida race. Photo by Matthew Rowe.

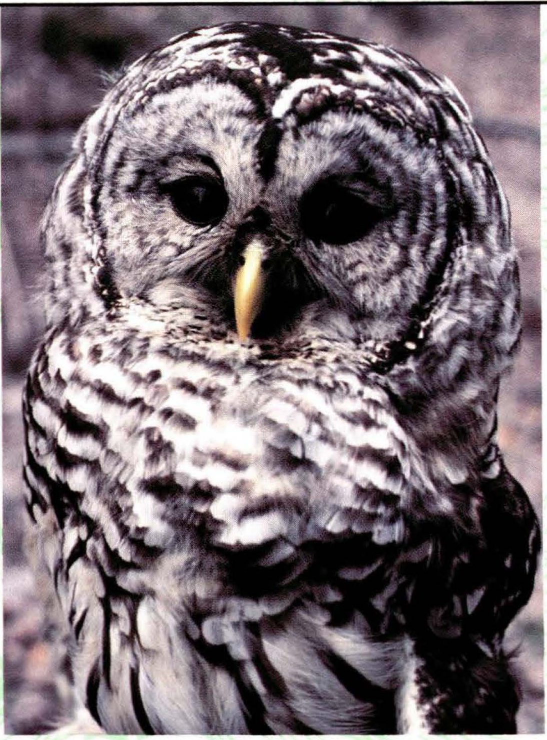
Black-and-white Owl (*Ciccaba nigrolineata*). Photo from Southern Quintana Roo, Mexico, by José Luis Rangel Salazar.

Mottled Owl (*Ciccaba virgata*). Photo from Tikal, Guatemala, by Richard P. Gerhardt.

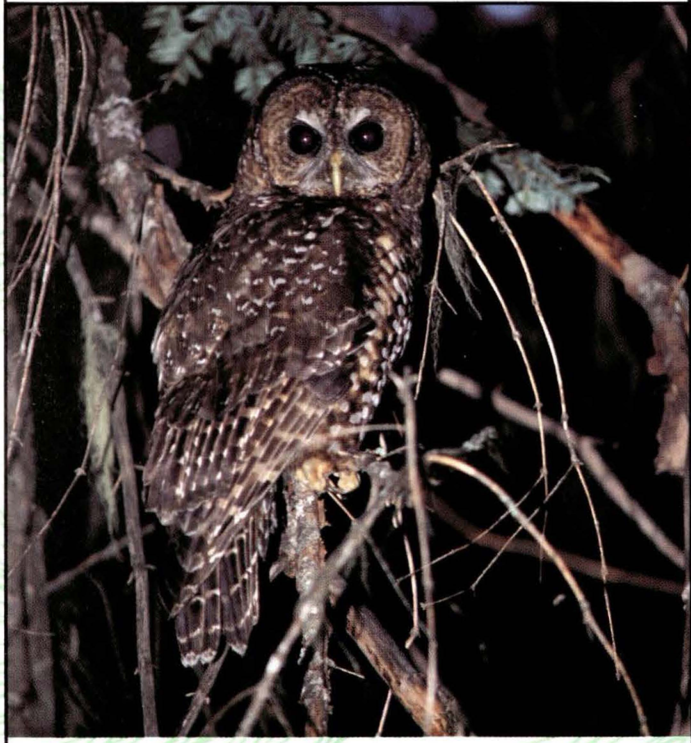
Spectacled Owl (*Pulsatrix perspicilata*). Photo by Katherine McKeever, The Owl Foundation.



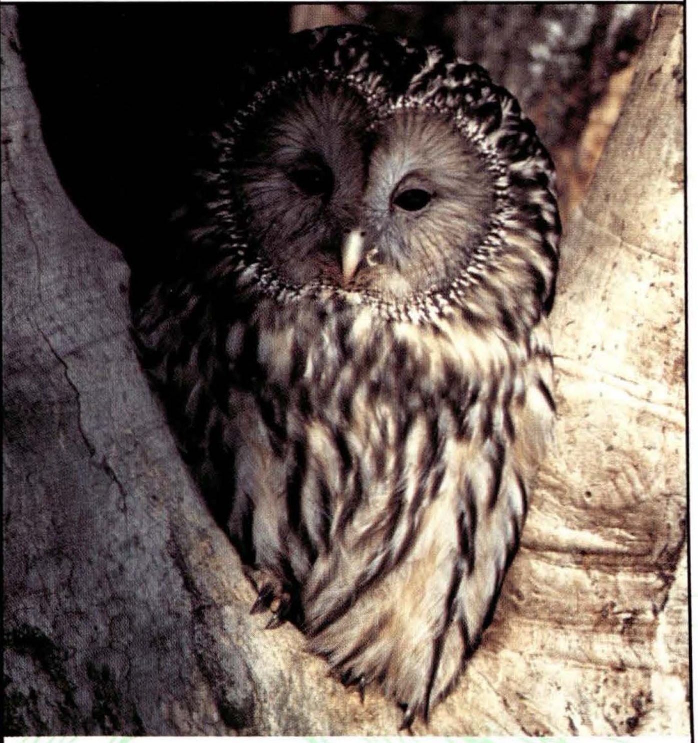
Tawny Owl (*Strix aluco*). Photo by Doug Ross.



Barred Owl (*Strix varia*). Photo from northern Minnesota, USA, by David H. Johnson.



Northern Spotted Owl (*Strix occidentalis caurina*). Photo by Rollin R. Geppert.

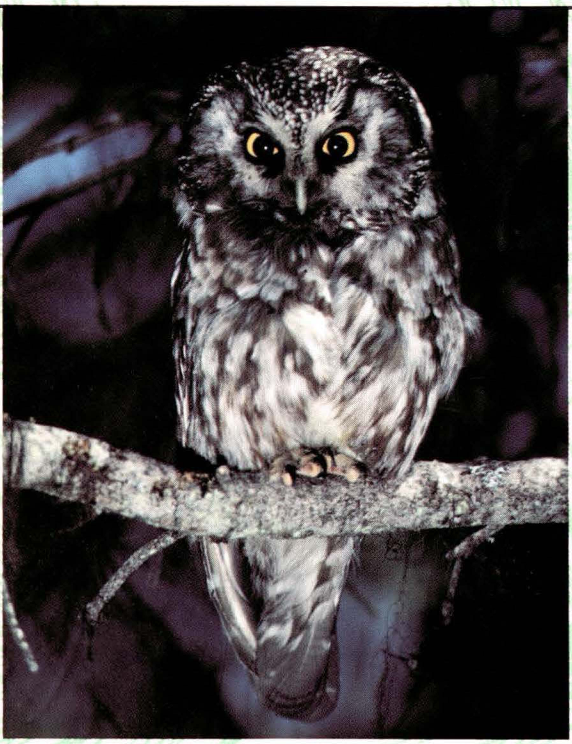


Ural Owl (*Strix uralensis*). Photographer unknown.

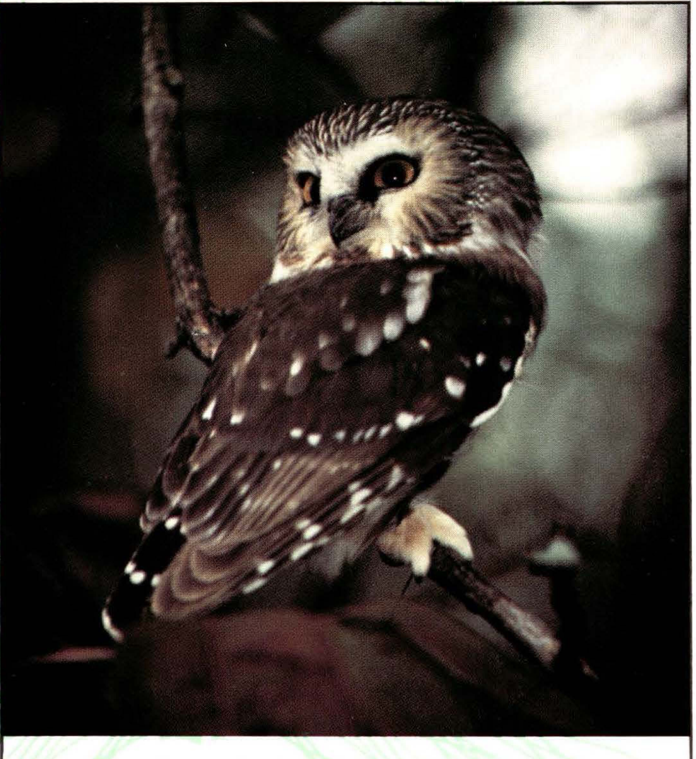
Great Gray Owl (*Strix nebulosa*). Photo by R.E. Gehlert.

Long-eared Owl (*Asio otus*). Photo of pair at nest by R.E. Gehlert.

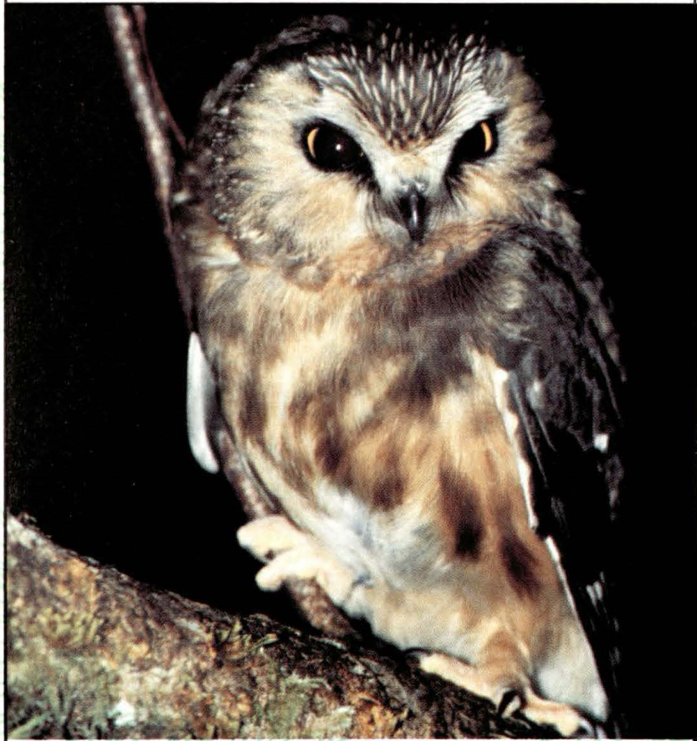
Short-eared Owl (*Asio flammeus*). Photo at Oak Hammock Marsh, Manitoba, Canada, by Gerry Jones.



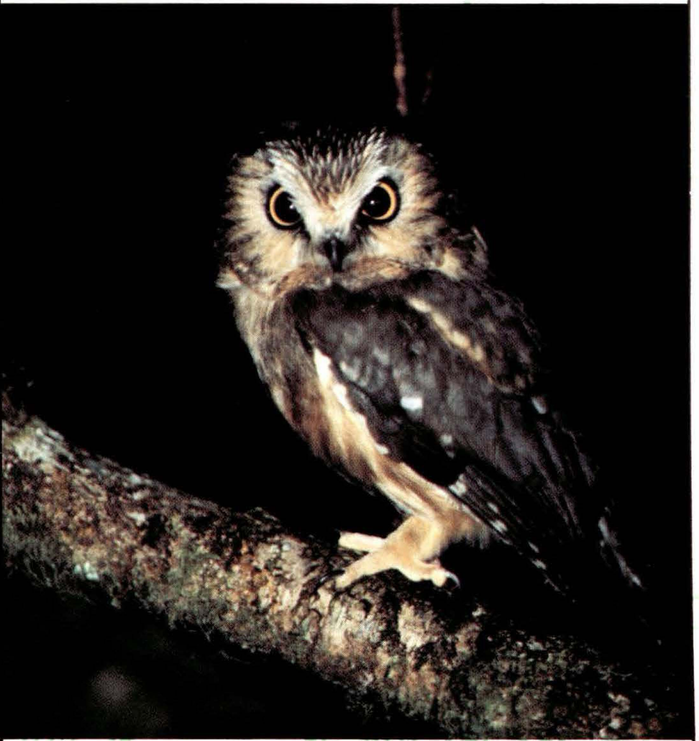
Boreal Owl (*Aegolius funereus*). Photo by Patricia and Greg Hayward.



Northern Saw-whet Owl (*Aegolius acadicus acadicus*). Photo near Green Bay, Wisconsin, USA, by Matthew Rowe.



Northern Saw-whet Owl, Queen Charlotte Island race (*Aegolius acadicus brooksi*). Photo by Matthew Rowe.



Northern Saw-whet Owl, Queen Charlotte Island race (*Aegolius acadicus brooksi*). Photo by Matthew Rowe.

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Official Opening Remarks: Manitoba Natural Resources

Merlin W. Shoesmith[1]

Mr. Chairman, distinguished guests, owl biologists, ladies and gentlemen. I am very pleased to be with you today to officially open the Second International Symposium on the Biology and Conservation of Owls. I welcome you to Manitoba and bring greetings on behalf of our Premier, Gary Filmon, and the Honorable Glen Cummings, Minister of Natural Resources. As well, a special welcome to the delegates from Europe, Asia, the United States, and delegates from across Canada. We appreciate the effort you have made to come to Winnipeg and I hope your stay in our province and your participation in this symposium will be enjoyable and memorable.

Memorable is a key word for me as I harken back 10 years to the First International Symposium on the Conservation and Biology of Owls held at the Viscount Gort Hotel here in Winnipeg. There are many returnees here today who either actively participated in the program or who took a lead role in the organization and arrangements of that symposium.

A lot of dedicated work has gone into organizing this event and I congratulate everyone involved. I understand that the art display and auction being held during this symposium features contributions by Manitoba wildlife artists and photographers. They deserve thanks for supporting the symposium.

Manitoba is among world leaders in focusing attention on owls with these symposiums. As well and since the First Symposium, Manitoba has passed a provincial Endangered Species Act. As Chair of the Committee that recommends designations of threatened or endangered species under the Act, I am pleased to report that Manitoba has had to place very few raptors on the endangered or threatened list. For example, 11 of the 12 species of owls that occur in the province are relatively secure in their habitat and require no extra legal protection.

The exception is the Burrowing Owl. Not so long ago we had several hundred breeding pairs in southern Manitoba. This species has rapidly declined to just a few individuals in the extreme southwest corner of the province. In spite of considerable effort and resources to turn around the decline, we as managers have not even been able to hold the line on maintaining a viable population.

Although we have designated this owl as endangered in Manitoba, we still face a major challenge of recovering it or saving it from extirpation on the landscape. It is our hope that the special session on this Burrowing Owl at this symposium will provide further insight and new ideas from you on how to save this species.

On the brighter side, we are fortunate to have a substantial population of Great Gray Owls in Manitoba. Based on the research carried out by Dr. Jim Duncan of the Wildlife Branch, this species has been "down-listed" from vulnerable to secure in Canada.

We are also fortunate to have a Great Gray Owl with us today. "Lady Grayl", who—as some of you will recall—was present at the 1987 owl symposium, and will be 13 years old this coming May. This magnificent bird has been maintained by Dr. Robert Nero of our Wildlife Branch, for education, research, and fund-raising. In addition to making numerous public appearances during our National Wildlife Week celebrations, Lady Grayl has given presentations in more than 150 schools throughout the province, thus capturing the hearts of many Manitobans. Bob assists her by driving the car!

Research studies and public relations work on the Great Gray Owl during the past 15 years by Bob Nero and his associates have brought this species into prominent public attention. There is little doubt that their efforts played a role in the selection of the Great Gray Owl as the official provincial bird emblem on 16 July 1987.

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[1] Assistant Deputy Minister, Manitoba Natural Resources, 200 Saulteaux Crescent, Winnipeg, MB R3J 3W3.

We feel under a special obligation to ensure that Great Gray Owls, and all other owl species, are secure. I hope that this symposium, in bringing together some of the best collective wisdom on owls, will provide decision makers with the basis for achieving sound recommendations to conserve owl populations.

In closing, I would like to express my gratitude to the several co-sponsors and contributors for their generous support that will make this symposium a success. It is with great personal pleasure that I now declare this second international symposium to be officially open.

Official Opening Remarks: Manitoba's Biodiversity and Sustainable Development

Brian C. Gillespie [1]

Thank you Mr. Chairman and thank you, Dr. Shoesmith, for your greetings and comments. On behalf of the Wildlife Branch, I, too, want to welcome everyone to Manitoba. I must say that I am overwhelmed by the extent to which the interest and excitement in northern forest owls that we saw here in 1987 has grown since that time. A lot has happened in owl research throughout the world, and a lot has happened in the management of Manitoba's natural resources in the last 10 years.

Not long after the 1987 owl symposium, our province embarked on a new initiative that was to guide us into the next millennium. On the heels of the 1987 Brundtland Report, we adopted that commission's principles of sustainable development. More than just a buzz word for the 1990's, sustainable development is a common sense approach that recognizes the connection between the well-being of people, the health of our environment, and the economy. I am pleased to announce that sustainable development strategies for fish and wildlife are to be developed for Manitoba.

Among the principles of sustainable development, we find requirements for local and international cooperation in the maintenance of biodiversity, research, and the development of comprehensive solutions to our problems. Hence, our gathering here today is one step in the on-going implementation of the principles of sustainable development. Further, following the UNCED Convention at Rio de Janeiro in June 1992, Canada, with Manitoba's active participation, initiated an inclusive process that culminated in the development of a Canadian biodiversity strategy.

We are proud of the fact that all jurisdictions in Canada have signed onto this document and have signed a statement of commitment that expresses our country's political resolve to implement the three main articles of Agenda 21 related to global biodiversity needs:

1. Conservation of biodiversity.
2. Sustainable use of biological resources.
3. Fair and equitable sharing of the benefits that result from the use of genetic resources.

These broad goals are being approached from an ecosystem-based management perspective which will form the cornerstone of our future resource management programming.

Notwithstanding our public commitment to move forward with this ecosystem-based management approach, it is with the full recognition that individuals and groups of species require intensive study to determine their place and future in the ecosystem. Owls, for example, are one of the yardsticks by which we will attempt to measure and constantly monitor ecosystem health and assist with future planning.

Manitoba's biodiversity contributes to global environmental health. A loss of diversity weakens entire natural systems, systems which humans depend upon. In Manitoba, to help maintain biodiversity in our resource-based economy, we look to new ways of doing our jobs. A landmark example is that our forestry planning is now based on ecosystem management, not tree stand management. In cooperation with the Manitoba Model Forest, we have also developed habitat models for 20 species of wildlife, including the Barred and Great Gray Owls. These models will be integrated with our forest resource inventory database.

When all is said and done, however, we have to be able to evaluate our efforts at maintaining biodiversity and a healthy ecosystem. Certain species, such as owls, are some of the best yardsticks for monitoring our success. I wish you well with your symposium. Your wisdom will guide us in our efforts to make our planet a better place for all living things. And in closing, I want to say thanks and congratulations to the many dedicated individuals who have worked so very hard at organizing this event. This is not an easy task. I am sure that the fruits of your efforts will be seen many times over as the events of the next few days unfold.

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[1] Director, Wildlife Branch, Manitoba Natural Resources, 200 Saulteaux Crescent, Winnipeg, MB R3J 3W3.

Official Opening Remarks: Bird Conservation in Canada

Michael S.W. Bradstreet[1]

It is my pleasure, as Executive Director of Bird Studies Canada (BSC), to take part in the opening ceremonies of the Second International Symposium: Biology and Conservation of Owls of the Northern Hemisphere. It is entirely appropriate that this symposium should take place in one of the colder cities in the Northern Hemisphere, in mid-winter, and it is fitting that temperatures have warmed substantially over the last few days to welcome international visitors. Even the owls are ready to cooperate, and Saturday's field trip promises great camaraderie and great views of Northern Hawk Owls, Great Gray Owls, Snowy Owls and perhaps others.

Bird Studies Canada was established by the Long Point Bird Observatory in 1994 to conduct and promote ornithological studies and to communicate the results to the public. BSC places emphasis on studies that increase understanding of avian distribution, abundance and population changes and their underlying causes and on studies that generate information in support of the conservation or preservation of Canadian birds and their habitats. BSC organizes, conducts, coordinates, and promotes research, surveys, monitoring programs and conservation studies that are international, continental, national, or regional in scope (i.e., usually not confined to one Province or Territory) and, whenever possible and appropriate, involve and promote a high component of volunteer participation.

BSC's affairs are governed by a Council appointed by the LPBO Board. The Council is currently chaired by Dr. J. Bruce Falls and includes representatives from across the country. Two Councilors are appointed by the Canadian Wildlife Service, the Society of Canadian Ornithologists and the Canadian Nature Federation (CNF). These appointments reflect BSC's interest in working in partnership with national government, academic, and conservation organizations.

Current national programs of BSC include Project Feeder Watch (PFW), the Canadian Lakes Loon Survey (CLLS) and the development of a network of migration monitoring stations across Canada. In PFW, up to 1,500 Canadians participate annually in bi-weekly counts of birds as part of a North American program to track winter birds that visit feeders. Volunteers in the CLLS monitor loon productivity on lakes across the country in relation to human impacts such as acid rain, shoreline development, and jet ski use. BSC is helping to develop a network of migration monitoring stations through development of standards, archiving and analysis of data, and by providing small grants through the James L. Baillie Memorial Fund.

The Baillie Fund was begun in 1976 with part of the proceeds of the annual Baillie Birdathon, a one-day sponsored bird count. Since then, the Fund has provided over $272,000 in support of 253 bird research and conservation projects in every province and territory. Of particular interest to this audience is our support for the development of a Boreal Owl breeding complex at the Owl Foundation, which you will hear more about from our banquet speaker, Kay McKeever, on Saturday. In addition, the Baillie Fund has supported status reports on Spotted Owl and Barn Owl habitat enhancement in British Columbia, Short-eared Owl research and conservation in Nova Scotia, Operation Burrowing Owl in Saskatchewan, migration studies of Northern Saw-whet Owls in Ontario, volunteer-based owl surveys in Manitoba, and educational programs on owls across the country.

Bird Studies Canada's international activities are coordinated through our designation, jointly with the CNF, as the BirdLife International partner in Canada. BSC and CNF are implementing BirdLife's Important Bird Areas program in Canada. The IBA program is an international conservation initiative designed to identify and protect critical areas of bird habitat worldwide. In Europe, the IBA program has demonstrably increased the protection of sites important for bird conservation. In Canada, where the program is just beginning, it has already attracted the support of government agencies, first nations and the birding public in British Columbia, Ontario, and Manitoba, where regional workshops have been held. We plan to hold additional workshops across the country in 1997 and 1998 and to publish a national directory of IBAs in 1999.

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[1] Executive Director, Long Point Bird Observatory and Bird Studies Canada, P.O. Box 160, Port Rowan, ON N0E 1M0 msxw@nornet.on.ca.

Through our BirdLife partnership, BSC has also been involved in research projects on three continents (in Mexico, Cuba, Laos, Malaysia, Indonesia, and Ivory Coast). In addition, we have initiated a program to train Latin American biologists in bird monitoring techniques through 1-month internships at Long Point Bird Observatory in Ontario. This CWS-sponsored initiative has already attracted participants from Cuba, Jamaica, Brazil, and Mexico and the demand for training is so large that we hope to help develop similar programs at additional sites across Canada.

Canada is a very large country and it is challenging to launch a new national initiative, especially in such challenging economic times. But I have been greatly encouraged by the support Bird Studies Canada is attracting. Already, our newsletter, BirdWatch Canada, is being read by over 5,000 Canadians who participate in our programs. It is clear that birds are important to Canadians. Bird images, including a Snowy Owl, grace our money and bird migrations grace our lives.

I wish all of you good science, good friendship and good birding over the next few days. And, on your behalf, I want to thank the organizing committee for bringing us all together to work for owls and their conservation.

BANQUET SPEAKER

Remaining Choices

Katherine McKeever[1]

The Owl Foundation is a place where one can watch the development of intimate relationships between individuals of most of Canada's owl species. The by-product is that recycled genes go back to wild populations in released progeny (table 1).

The physical property, about 4 ac (1.61 ha) is equally divided between a forested slope (remnant Carolinian vegetation zone) and new grassland recovered from former orchards. Geographically, we are on an ancient lake bed between the Niagara Escarpment and the south shore of Lake Ontario. Our forest slopes down from 100 ft (30.7 m) to a wide river estuary. Many of our old trees are 120 ft (36.9 m) tall with a girth of 12 ft or 3.8 m. Our latitude is the most southern in Canada (in line with Roseburg, Oregon) and our climate the most moderate in Eastern Canada. This permits all Canadian owl species, except the insectivorous Flammulated Owl (*Otus flammeolus*), to be maintained outdoors the year round.

In 1965, we embarked on a modest plan to attempt rehabilitation of injured owls to the point of responsible release. Now, 3,600 owls later, all but local owls arrive from across the continent already assessed as permanently damaged, in the hope that some use can be made of their lives.

Our challenge is to attempt the best recovery of lost faculties and broken spirits by providing the opportunity for making their own choices in every aspect of their lives. These choices include the ability to move from one defined space to another, and yet to another, through overhead corridors; to meet others of their species; to choose a territory; to select every

Table 1.—*Canadian owl species which have produced living progeny at the Owl Foundation in Ontario, Canada.*

Owl species	**No. of successful pairs**	**Span of breeding years per species**	**Approximate no. of young raised**
Snowy Owl (*Nyctea scandiaca*)	6	'78/'96	57
Great Horned Owl (*Bubo virginianus*)	4	'84/'96	34
Great Gray Owl (*Strix nebulosa*)	4	'85/'96	23
Barred Owl (*Strix varia*)	4	'90/'96	9
Barn Owl (*Tyto alba*)	3	'74/'94	200
Long-eared Owl (*Asio otus*)	1	'95	1
Northern Hawk Owl (*Surnia ulula*)	3	'87/'96	34
Eastern Screech-owl (*Otus asio*)	9	'76/'96	118
Burrowing Owl (*Speotyto cunicularia*) (Great Plains race)	21	'82/'96	131
Boreal Owl (*Aegolius funereus*)	3	'83/'87	7
Northern Saw-whet Owl (*Aegolius acadicus*)	6	'79/'96	51
Flammulated Owl (*Otus flammeolus*)	2	'92/'93	1
Northern Pygmy-owl (*Glaucidium brasilianum*)	3	'85/'90	9

N.B. - Short-eared Owls (*Asio flammeus*) have produced eggs but not living progeny.
- 3 Spotted Owls (*Strix occidentalis*) have been residents but never two at the same time.
- One male Snowy Owl, wing-crippled in Alberta in 1965, in adult plumage, has sired his first chick in 1996!

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[1] The Owl Foundation, 4117 21st Street, R.R. 1, Vineland Station, ON, Canada L0R 2E0.

size and type of roost, of all heights, of exposure or seclusion; to select from two to four available nest sites in each territory; to be alone or in company.

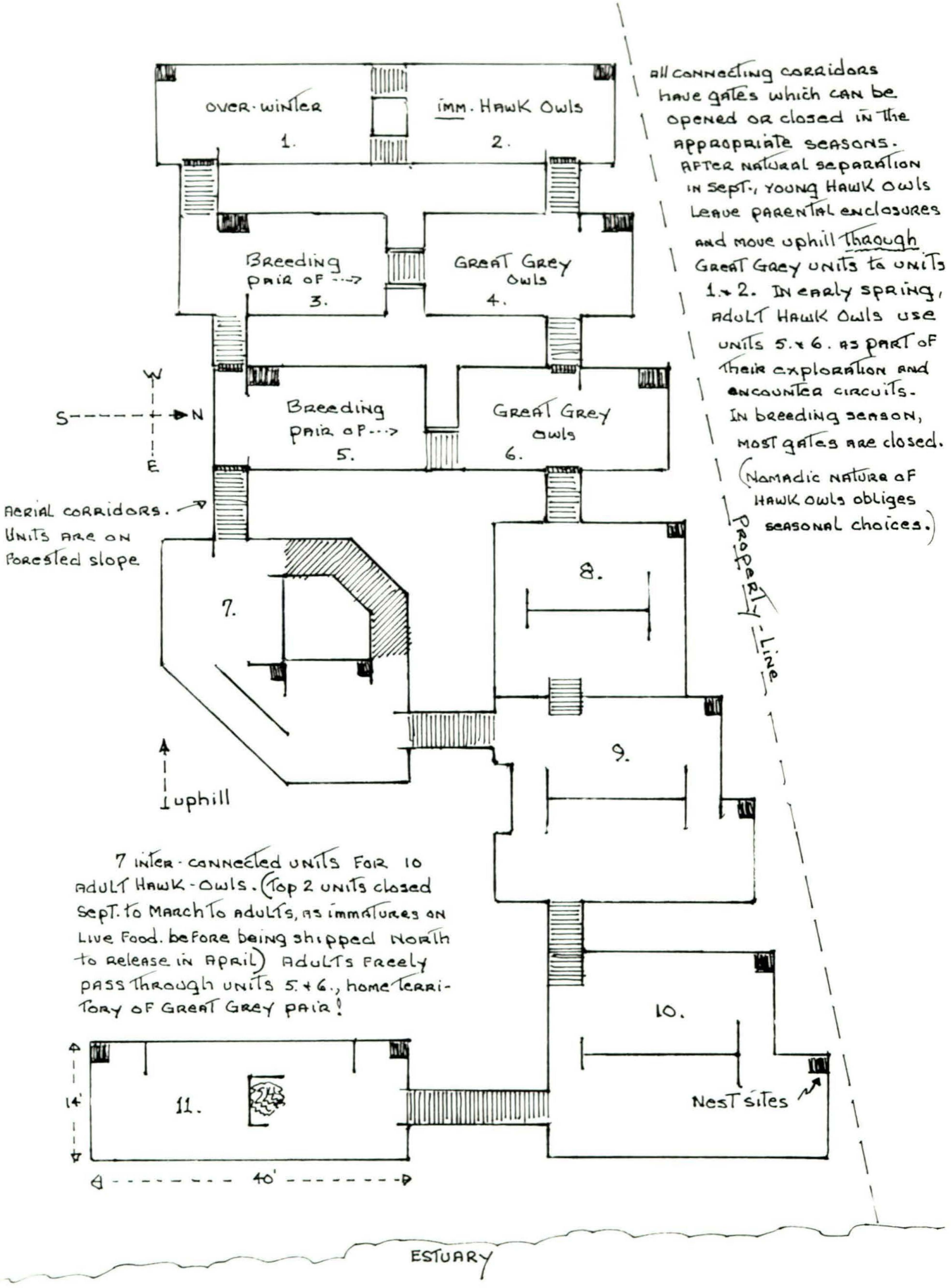
All of this involves withdrawal from public visitation and opens the need for private funding, since these are inherently wild but traumatized owls and spaces for recovery must be very large. This need is not just to promote the likelihood of ultimate breeding, but also to provide a suitable habitat for young owl's early experiences. A breeding pair of Snowy Owls (*Nyctea scandiaca*), even when the female is a flightless cripple, needs a minimum of 1,200 ft^2 (111 m^2). A pair of Great Gray Owls (*Strix nebulosa*) 1,000 ft^2 (92 m^2) and for them an open forest setting and cage heights to 18 ft (5.5 m). Even a wing-crippled hawk owl (*Surnia ulula*) will promptly climb 16 ft (4.8 m) to a semi-cavity nest site. In forest owls, height is security, and we must provide 'furniture' for their use in reaching acceptable levels. Finally, since these enclosures will be the first exposure to surroundings for the off-spring, they must also be able to contain live prey species, in suitable cover, which the male can catch. This is critical to the development of a memory that food moves and makes noises, food is brown and food fights back!

In our efforts to expedite breeding, after much trial and error, we have evolved a typical breeding complex to be made up of three large, double compounds, linked to each other by flight corridors. Into it we put six owls of one species, both sexes, and all corridors open. We seldom know whether the occupants have had previous pair-bonding experience in the wild (of species which tend to form life bonds) a factor that may delay new bond formation as the now captive partner apparently waits for that bond to dissipate before beginning negotiations with a new individual. Even if several had experience of previous bonds, it is seldom over 4 years before the new pair will have formed a liason and claimed one of the compounds. With luck, a second pair will form in another year or so, but of course the remaining two owls are relegated to the third compound, not by choice but by being the residue of the first two choices! This is not a popular position for anyone, owls included. They are removed from the complex and put into another mixed rotation elsewhere. This frees the remaining compound and it is reserved for the progeny of the two pairs.

At our latitude, August is departure time from parental territories for the young. It is interesting to note that the young from both pairs have found their way to the free territory by September, and that the parents never follow. The corridors are then closed and the assembled young must learn to fend for themselves on live prey tossed into natural cover. Defrosted rodents are provided (visibly) for the three coldest months, with live feeding resuming in early spring, when most young are spontaneous and successful hunters. It should be noted that this schedule applies only to northern species, which are shipped by air to parental sources in spring. Progeny of owls of our latitude are released in the September of their natal year, following 1 month on live prey. The offspring of species which engage in fast flight or long distance travel (Hawk Owls, Snowy, Great Horned) may be moved in spring to enclosures which offer sustained flight over 80 to 96 ft (24 to 29 m) to build up pectoral muscles in pre- paration for this challenge.

Hawk Owls are irregular in many ways, one of which is the inclination to form only seasonal bonds with each other, appearing not even to recognize, by October, the partner of last April! This inconstancy presents unique challenges in designing a cage labyrinth conducive to breeding. At our facility, 10 Hawk Owls can access seven enclosures and can fly a total circuit around 0.5 ac (0.2 ha) via the corridor system (figs. 1, 2, and 3). Females of this species appear to develop a fidelity to a nest site in a given territory, if not to a male. Wing-crippled females, finding corridors inaccessible will stay home and loudly solicit for a male, while flighted females use the corridors to go 'shopping' for males, cause all kinds of conflict with both males and females along the way, and invariably bring the selected male back 'home'! Apparently few males can resist a soliciting female!

Finally, the surprising, even astonishing, demonstrations of bonding between self-selected individuals can only be seen, year round and through their remaining life times, on a remotely controlled monitoring system. Thus up to 23 video cameras, rotated by season amongst 30 of our 52 enclosures, routinely relay images of private lives. Unlike the confrontation inevitable with human presence, the owls are unwitting of this surveillance.


OVER-WINTER
1.
IMM. HAWK OWLS
2.
Breeding pair of --->
3.
GREAT GREY OWLS
4.
Breeding pair of --->
5.
GREAT GREY OWLS
6.
W
S
N
E
7.
8.
9.
10.
11.
uphill
Nest sites
14'
40'
ESTUARY
PROPERTY-LINE

All connecting corridors have gates which can be opened or closed in the appropriate seasons. After natural separation in Sept., young Hawk Owls leave parental enclosures and move uphill through Great Grey units to units 1.+2. In early spring, adult Hawk Owls use units 5.+6. as part of their exploration and encounter circuits. In breeding season, most gates are closed. (Nomadic nature of Hawk Owls obliges seasonal choices.)

Aerial corridors. Units are on forested slope

7 inter-connected units for 10 adult Hawk-Owls. (Top 2 units closed Sept. to March to adults, as immatures on live food before being shipped North to release in April) Adults freely pass through units 5.+6., home territory of Great Grey pair!

Figure 1.—*Diagram of 0.5 ac (0.2 ha) complex for five pairs of nomadic Hawk Owls (*Surnia ulula*) at the Owl Foundation in Ontario, Canada.*

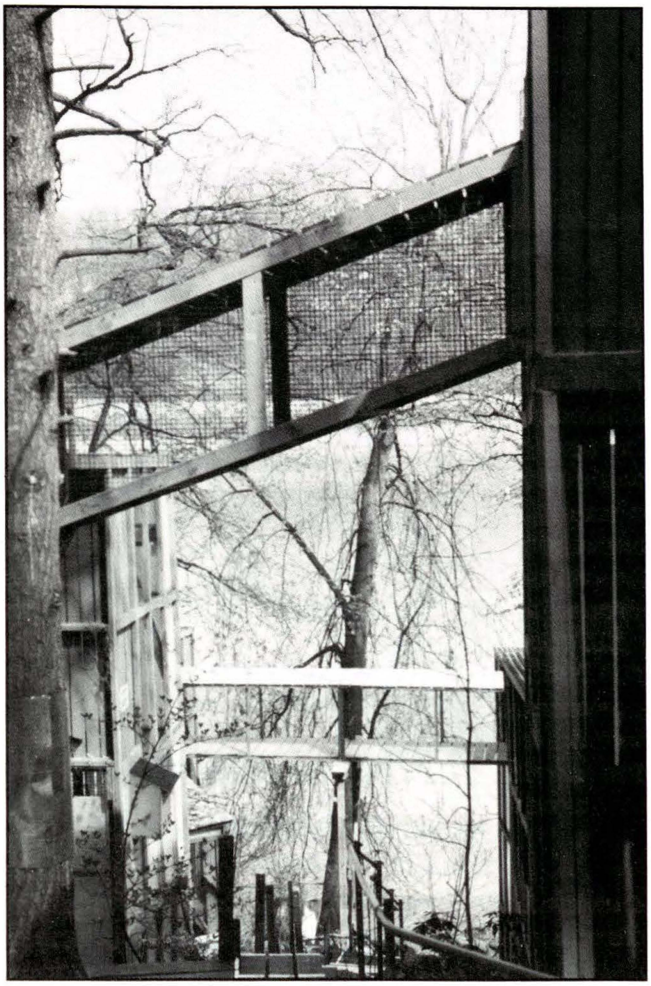


Figure 2.—*Two of six flight corridors connecting 7-unit Hawk Owl (*Surnia ulula*) complex at the Owl Foundation in Ontario, Canada.*

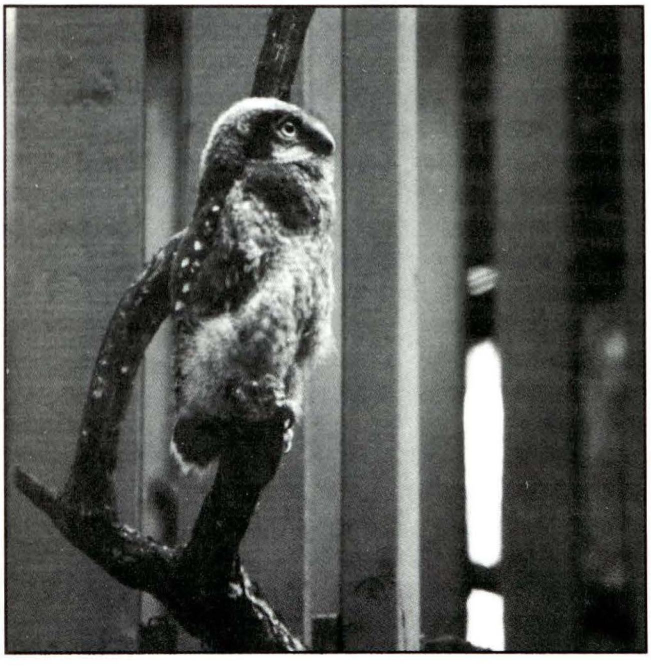


Figure 3.—*Juvenile Hawk Owl (*Surnia ulula*) typically on vertical snag in parents' compound at the Owl Foundation in Ontario, Canada.*

Of course springtime is the season when one hovers hopefully around the monitors as the breeding behavior unfolds, watching for the first glimpse of irresistible fuzzies and admiring the total devotion of both parents (figs. 4, 5, and 6). Anticipation of these exciting moments is part of all our winters, even as we review the tapes of previous seasons.

But for the most memorable moments, there is nothing so touching, relayed through the camera's eye, as a pair of middle-aged Great Gray Owls, sitting close together in December sunlight (when egg follicles and gonads are at their lowest ebb) grooming each other quietly and solicitously, keeping the pair bond in good order. For the watcher who has kept the dream alive for so many years, trying and failing and trying again, these are the golden moments. Against all predictions, such permanently damaged wild owls have overcome their physical deficits, have left fear and stress behind, and are utterly absorbed in each other. Over the years it has been a privileged look at ancient relationships, still enduring, still strong, even after such calamitous lives.

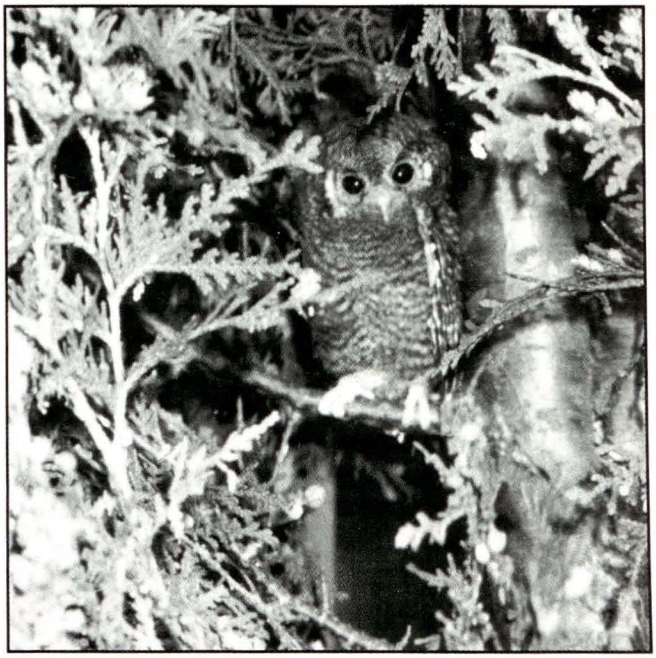


Figure 4.—*Just fledged juvenile Flammulated (*Otus flammeolus*) Owl at the Owl Foundation in Ontario, Canada.*

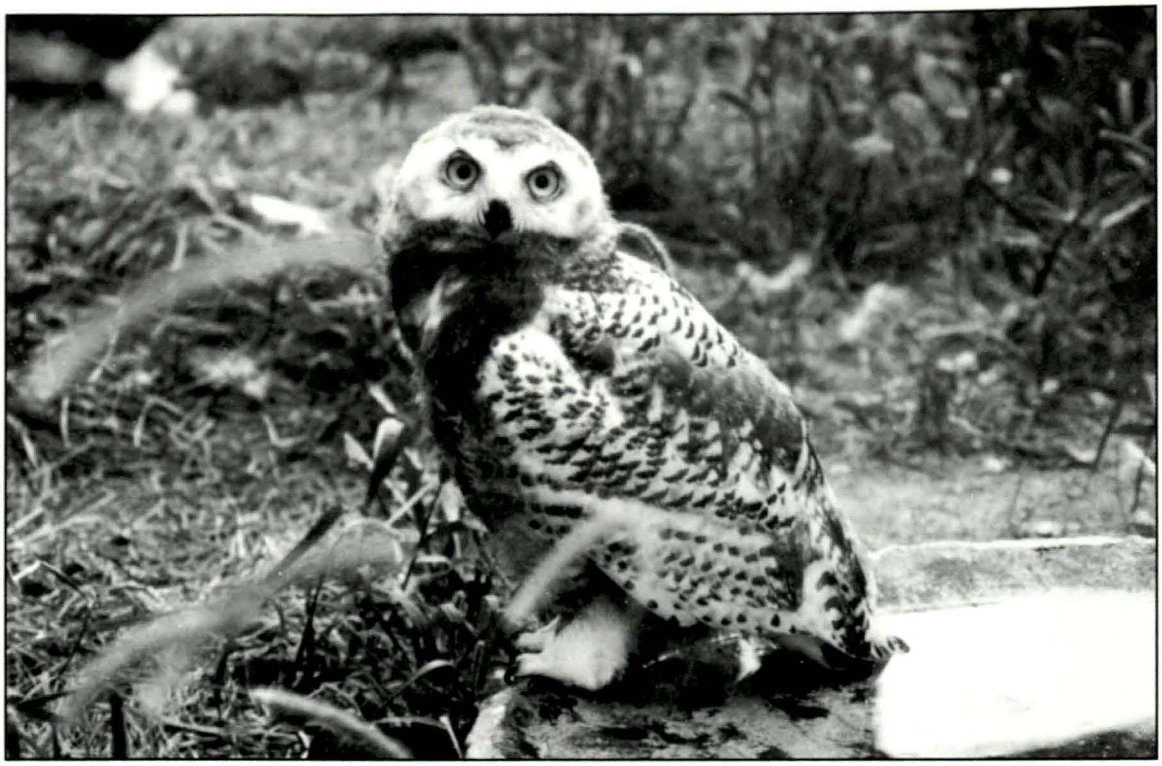


Figure 5.—*Immature Snowy Owl (*Nyctea scandiaca*) on pool in parents' 1,200 ft² enclosure at the Owl Foundation in Ontario, Canada.*

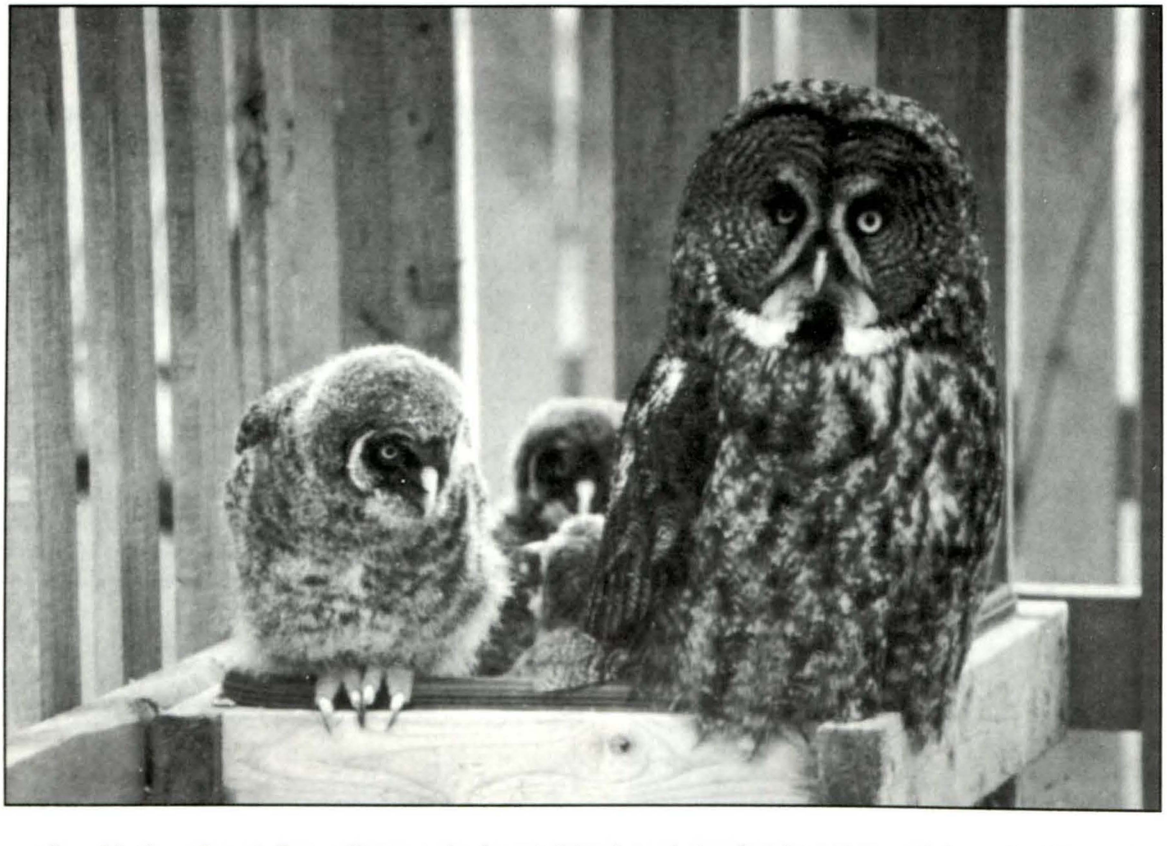


Figure 6.—*Mother Great Gray (*Strix nebulosa*) (blind and deaf right side) with brood of 3 nestlings at the Owl Foundation in Ontario, Canada.*

Summary and Concluding Remarks

Richard J. Clark[1]

Abstract.—Ten years have elapsed since the first International Owl Symposium was held in Winnipeg. The number of topic species was expanded from 22 (1987) to 61 (1997) and the topic was broadened from owls of the northern forest to those of the northern hemisphere. The number of studies reported expanded from 38 studies (mean = 5.76 years for study period duration) to 101 studies (mean = 4.89 years per study). Fifteen species were reported on in 1987 and 17 species in 1997. The Northern Saw-whet Owl (*Aegolius acadius*) was the most reported species in 1997 and the Boreal or Tengmalm's Owl (*Aegolius funereus*) in 1987. A plea is made for more research on owls in lesser-known parts of the World and for conferences to call attention to those parts of the World where research is being conducted or needed.

SUMMARY

With Comparisons to 1987 Conference

It was an honor to be asked to summarize the 1987 Conference and I have been doubly honored to provide the summary and concluding remarks for this conference as well. For those readers of this report who attended the banquet, you will note some differences between the two. At the banquet my emphasis was (a) to provide the results of numerical "analysis" pertaining to the species reported on, geographic areas of study, etc. and (b) to urge researchers to become more actively involved in the conservation of owls in general and the owls that they are working on specifically. I tried to convince the listeners that while there were some great studies reported on here, there is perhaps an even more urgent need to address research to the southern hemisphere, especially in tropical Africa and the countries of the southwestern rim of the Pacific.

Returning to Manitoba is somewhat like "coming home" to me, having spent a couple of field seasons researching the Short-eared Owl[2] in the "bust" year of 1968 and the "boom" year of 1969. It was bust and boom for both the Microtine rodents and the Short-eared and Long-eared Owls as well as Northern Harriers (*Circus cyaneus*) that availed themselves of the great food availability in 1969 on the Manitoba prairies. Before the banquet a tall gentleman came up to me and asked me if I knew of anyone who could tell him about trapping Great Gray Owls. Very conveniently Bob Nero was standing nearby and I offered to introduce him to Bob. He then ended the joke on me by reminding me that he was Herb Copland and I realized that I had "been had." When I came to Manitoba, Bob Nero was one of the first people that I turned to for assistance in becoming familiar with the local scene and he was most generous in offering that. Herb was in charge of the nest record program and he also generously shared information from that program.

When my family and I left Manitoba in 1969, we headed west and enjoyed the warm hospitality of Mary and Stuart Houston in Saskatoon. Stuart was very busy then banding the many owls that resulted from the very high Microtine rodent population that Saskatchewan was also experiencing. It was a personal pleasure to hear Stuart report on about 50 years of banding here at the conference. In addition to the thousands of owls that he has banded, he has established a network of farmers and young banders which has, no doubt, benefited those cooperators in ways in which they probably do not even realize. His is a model that is well worth emulating by other researchers and conservationists.

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[2] See Appendix for a complete listing of owl species of the world common names and binomials taken from Sibley (1996).

Bob Nero and Lady Grayl have also set a fine example in the realm of conservation and probably few know about the thousands of dollars that they have raised for conservation and education projects, by visiting schools. Bob is no doubt aware of the role that the youth of Canada will play in its future and his and Lady Grayl's investment of time and effort, like Stuart's, is bound to pay large dividends in the future. It is heartening to see Bob "passing the baton" on to Jim Duncan. It seems apparent to me that Bob's "fingerprints" are on Jim when it comes to a respect for the resource that has brought us all here, i.e., owls. Jim's respect and passion, I am sure, goes beyond owls to the natural environment.

Another Canadian that I have had the privilege of knowing and working with is Katherine McKeever from Ontario. Kay and Larry have built a world-class facility for owl research. It started out as a raptor rehabilitation operation but shifted to just owls and then again to a captive-breeding facility and then to what it is now—a fine facility for behavioral research on owls. I would encourage anyone interested in doing basic behavioral research on owls to contact Kay. While I have focused on just a few giants in the field of owl research that I have had the privilege of knowing and working with, I am sure there are many others that I have omitted, simply because I have not had the pleasure of knowing them. And while I have dwelled on those with longer track records, there is plenty of cause for optimism with a very healthy crop of younger researchers evident at this conference.

One other comment by way of reminiscences has to do with the field trip to the boreal forest. I became very familiar with the grassland and aspen-parkland while working in Manitoba but did not become exposed to the boreal forest. On Saturday, three bus-loads of participants journeyed north to the Pine Falls area. It was a sunny, mild day with little wind and Microtine rodents had obviously done their thing which set the stage for a superb owling day. I personally saw, between conversations, 12 Northern Hawk Owls, 4 Great Gray Owls, and 4 Snowy Owls. It was also a good opportunity to enjoy a good look at the terrain that developed as a result of glaciation of the old lake bed of Lake Agassiz.

MATERIALS AND METHODS

The material presented here is the result of the 1987 conference publication and the program and abstracts prepared for this conference. To be more comparable I should have used the programs for both conferences, but could not locate my earlier conference program. The analysis is only meant to show any major trends; it is what is available in those two documents, although an attempt was made to hear as many presentations as possible. Concurrent sessions this time, however, prevented my hearing them all. The number of topic species was expanded from 22 (1987) to 61 (1997) and the topic was broadened from owls of the northern forest to those of the northern hemisphere. The number of studies reported expanded from 38 studies (mean = 5.76 years for study period duration) to 101 studies (mean = 4.89 years per study) as shown in figure 1. The percent of studies for each duration period are shown for more direct comparison. In both cases one-year studies were the most frequent case with there being about a one-year average shorter duration for those studies reported in 1997.

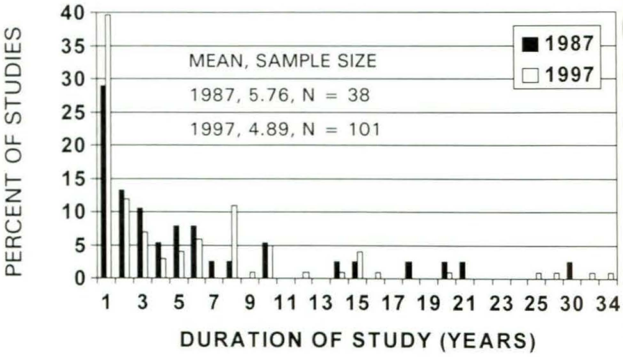

Figure 1.—*Study period duration for research reported at the 1987 and 1997 owl symposium conferences compared. Note that the number of studies for each time period are percentages for direct comparison. Note also the discontinuity for the "Years of Study" scale.*

The topics reported on are analyzed for those species that were candidates for both conferences (table 1) and then for those species that were added (table 2) for inclusion in this conference; i.e., northern hemisphere species, not just those of the northern forest. In table 1

Table 1.—*Summary of owl symposium papers, subject species (according to the 1987 species list) and topic(s) reported on, for the 1987 conference compared to 1997. Total number of studies reporting are listed as 1987/1997 for comparison.*

	AN[1]	DI	BB	FH	HA	NB	PO	R-T	T-P	TN
Flammulated Owl		1/	2/1		1/4	1/	1/			4/5
Eastern Screech-owl		1/	2/3	1/1	2/		1/	1/	4/	5/4
Western Screech-owl			/2	/1	/1					1/4
Common Scops-owl										1/
Striated Scops-owl										1/
Oriental Scops-owl										1/
Collared Scops-owl										1/
European Eagle-owl				1/			/2	1/		3/1
Great Horned Owl	3/			/2	1/	1/	1/5			7/7
Blakiston's Fish-owl										1/
Northern Hawk Owl	2/	/3	4/	1/	1/	4/		1/		8/3
Northern Pygmy-owl	1/									2/
Eurasian Pygmy-owl			1/	1/					1/	3/
Oriental Hawk Owl										1/
Barred Owl	2/		1/2		5/2	2/1		2/	1/	9/6
Spotted Owl		1/2	2/4	/1	1/2	2/		2/	1/	3/11
Great Gray Owl	2/1	2/	1/1/	5/1	7/1	4/	2/4	3/		12/8
Tawny Owl		/1	1/1	3/2	2/	1/	/1			4/5
Ural Owl			2/	1/2	1/	1/	/2	1/		3/4
Long-eared Owl	3/		1/1				/4			5/5
Boreal or Tengmalm's Owl	4/	3/	5/7	1/	5/	3/	1/3	2/	1/	14/10
Northern Saw-whet Owl	3/1		2/8	2/	4/	1/	1/3	1/	1/	9/12
	20/2	8/6	24/30	16/10	30/10	20/1	7/24	14/	9/	98/80

[1] Legend: ANatomy, DIstribution, Basic Behavior, Food Habits, HAbitat, Nesting Biology, POpulations, Radio-Telemetry used, Tape-Playback, Total Number of studies reporting.

there was a decline in those reporting on anatomy, habitat, and nesting biology. There were no studies in this species list that indicated using either radiotelemetry or tape-playback techniques. There was a slight increase in studies that reported on breeding biology and a more than triple increase of population-centered studies. There is a suggestion that studies on the Northern Hawk Owl have declined but a good sign in the increase in the number of studies on the Western Screech-owl and, not surprisingly, the Spotted Owl.

Those species reported on in 1997 but not eligible for reporting in 1987 are summarized in table 2. There is a notable exception. The Lanyu Scops-owl, which may be a race of the Elegant Scops-owl (*Otus elegans botelensis*) or may represent a separate species, is definitely an owl of the northern hemisphere and was inadvertently left off the candidate list. Severinghaus has continued her earlier work (1989) on this form which has been listed as endangered (King 1981). She provided us with a detailed report on the population dynamics, productivity and status of this owl. There were a healthy number of studies reporting on basic behavior, food-habits, habitats and the number reporting on population phenomena had more than tripled. Species emphasized included the Barn Owl and Burrowing Owl. No studies on "new" species using either radiotelemetry or tape-playbacks were reported.

All of the above has been fairly objective, but now I will become a bit more subjective. Examining just the titles in the 1997 program there are over 20 in which only the common name is given for the owl(s) reported on. If the reporter's goal is to reach as wide an audience as possible, then using the international language of biologists; i.e., the binomial, would

Table 2.—*Summary of owl symposium papers, subject species (according to the 1997 species list) and topic(s) reported on.*

	AN[1]	DI	BB	FH	HA	NB	PO	R-T	T-P	TN
Barn Owl					1		6			6
Ashy-faced Owl										
African Grass-owl										
Mountain Scops-owl										
Balsas Screech-owl										
Pacific Screech-owl										
Whiskered Screech-owl										
Vermiculated Screech-owl										
Tropical Screech-owl										
Bearded Screech-owl										
Bare-shanked Screech-owl										
Puerto Rican Screech-owl										
Bare-legged Owl										
Crested Owl										
Spectacled Owl										
Spotted Eagle-owl										
Spot-bellied Eagle-owl										
Brown Fish-owl										
Tawny Fish-owl				1						1
Snowy Owl			3	1			1			5
Brazilian Pygmy-owl										
Ferruginous Pygmy-owl				1	1					3
Collared Owlet										
Javan Owlet										
Elf Owl										
Little Owl										
Spotted Owlet										
Burrowing Owl		1	3		1		3			8
Mottled Owl	1									1
Black-and-white Owl	1		1							2
Brown Wood-owl										
Hume's Owl										
Fulvous Owl										
Stygian Owl										
Striped Owl										
Short-eared Owl							2			2
Marsh Owl										
Jamaican Owl										
Unspotted Saw-whet Owl										
	2	1	7	3	3		12			28
	4[2]	7	37	13	13	1	36			108

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[1] Legend: ANatomy, DIstribution, Basic Behavior, Food Habits, HAbitat, Nesting Biology, POpulations, Radio-Telemetry used, Tape-Playback, Total Number of studies reporting.

[2] Note subtotals for those species that were listed for the 1987 conference and reported on there also are carried forward from table 1.

seem to maximize his/her chances. That goes also for reaching the reading audience as well, for if only the title is picked up in electronic retrieval then the audience potentially expands greatly by including the binomial(s) in the title. There were over a half dozen in which no name was given at all, neither common nor binomial. This is not offered as criticism but rather a suggestion to think biologically and globally.

Looking at the geographic regions of the study locations (fig. 2) one can see that the expected large number of papers dealing with the United States and Canada was realized. While reports of studies originating in Scandinavia included papers from Finland, Norway, and Sweden in 1987, only studies from Finland were reported in 1997. Reports from other countries in 1987, but not reporting in 1997, included those from Germany, Spain, and the former USSR. Reports from countries not reported on before included those from the United Kingdom, Belarus, Taiwan, Costa Rica, France, Japan, Malawi, the Republic of Russia, and Guatemala.

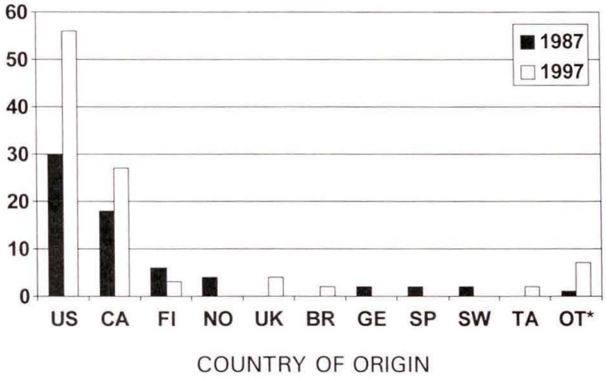

Figure 2.—*Country of origin for studies reported on for 1987 and 1997 compared. Country Legends are: US = United States of America, CA = Canada, FI = Finland, NO = Norway, UK = United Kingdom, BR = Belarus, GE = Germany, SP = Spain, SW = Sweden, TA = Taiwan and OT* is one report each from Africa, Costa Rica, France, Guatemala, Japan, Malawi, and USSR (1987).*

CONCLUDING REMARKS

This section will deal with a summary of owls of the world with a hope that the energies, enthusiasm, format and willingness to share with others from these two conferences and dealing with both the biology and conservation of owls will spread to other parts of the globe. There is no question in my mind that the format of them (a) has been one that has had an effect on the resource that we report on, i.e., the owls, and that (b) it should be emulated in other areas where the pressures on the owls is even greater than in the northern hemisphere. The owls are less known, more concentrated and in areas where the human population is typically more dense.

A comparison of the owls of the northern and southern hemispheres (table 3) shows that more than twice the land mass above water is found in the northern hemisphere while only 2 percent more owl species are confined to the northern hemisphere. One can also see that, on a percentage basis, more than twice as many owls of the southern hemisphere are threatened. Threatened, as used here, is that of the IUCN Red Book and does not indicate the level of threat (Sibley, pers. comm.).

Looking further at conditions that contribute to the threatening of owl species, Marcot (1995) has summarized very nicely the owls that are of old-growth forests in the world. He indicates that 83 of the total owl species of the world are

Table 3.—*Extant owls[1] of the northern and southern hemispheres compared.*

Hemisphere	Percent of land mass	No. spp.[1]	No. threatened[1]
Northern	67.8	78 (39)[2]	11 (14.1)
Southern	32.8	62 (37)	13 (28.9)
Both	100	60 (30)	1 (1.6)

[1] Compiled from Sibley (1996).

[2] Values in parentheses are percentage.

"closely associated with old, dense, or undisturbed forests... ." Of those 83 species, 26 species (31.3 percent) are found on islands or peninsulas, while 57 (68.6 percent) are found in continental situations (fig. 3). In addition, out of the last six extinctions, five (83.3 percent) were of owls associated with old-growth forests in island situations. If we are prone to think of this harvesting of old-growth forest as only important in the southern hemisphere, I will quote from an abstract of a paper presented at this conference. Mossop (1997) states "Pressures are building for human harvest of both old and larger trees, even in the northern extremes of the boreal forest."

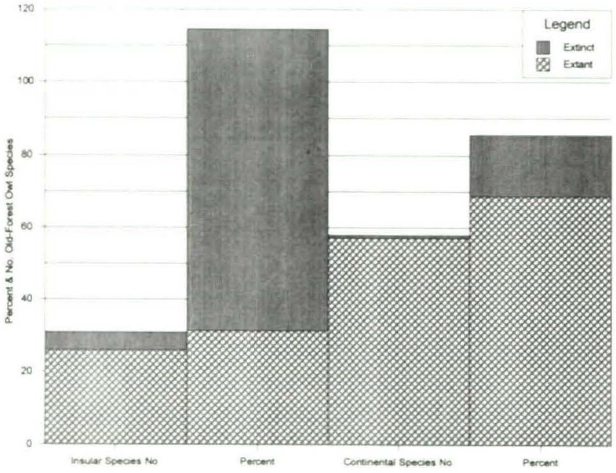

Figure 3.—*Number of island (insular), old-forest owl species that currently exist (extant) versus those extinct, compared to those of continental settings (after Marcot 1995).*

Turning to another facet of the global situation; i.e., the human population, Senator Gaylord Nelson of Wisconsin, founder of the Earth Day concept and now retired, gave raptor biologists something to think about. Speaking at an annual conference of the Raptor Research Foundation he invoked the "Rule of 70 Rule" which states that if you divide the annual growth rate of a population into the number 70 you will obtain the doubling time for that population. Realizing that the human population varies from region to region and country to country he used 50 years for the doubling time of the U.S. population (it is shorter for the World as a whole). He reminded his audience that with a population doubling, if you consider all of the things that are now used by the existing population, they will also have to be doubled, unless the quality of life is to be diminished. That is, that population will need twice as many residences, twice as much transportation facilities, and twice as much food.

Brewer (1994) points out that humans expropriate (as of 1986) by direct use, co-option or by missing production, 41 percent of the potential new primary production of this planet. Direct use was only 3.2 percent with the remainder being either co-opted; i.e., on lands that are strictly dedicated to human use or missing production. In the latter category are declines resulting from (a) agriculture; e.g., cornfields versus tall grass prairie; (b) conversion of forest to pasture; (c) conversion of natural vegetation to malls, highways, factories, university research parks, etc.; and (d) desertification that has accompanied human occupation of dry savanna and grassland.

Before I am stereotyped as a doomsday biologist I would point out that I do believe that the present trends can be turned around. I will quote another abstract (Takats *et al.* 1997) which points out the purpose for setting up a model forest; i.e., to "develop and recommend an approach to sustainability and integrated resource management through research and technology developed by means of collaborative partnerships." If the human population is to turn things around some of the critical ingredients for accomplishing it are contained in that statement of purpose.

Where do we go from here? It is heartening to see reports of research that is penetrating the vast realm of the unknown of the owls, and our, world; e.g., Butynski *et al.* (1996), Enríquez Rocha and Rangel (1997), and Gerhardt and Gerhardt (1997). Enríquez Rocha and Mikkola (1997) have attacked a new frontier with their sociological study of man's perception of owls in Central America and Africa. This a necessary groundwork for education on owls and humans and the environments that we share.

New basic understandings of the Ferruginous Pygmy-owl have been presented by Proudfoot (1997a, 1997b). A healthy discussion about an unhealthy subject resulted from the Burrowing Owl Conservation Workshop. The species is definitely in need of considerable assistance in the northern limits of its range in North America; i.e., southern Canada as well as elsewhere; e.g., parts of California. The embryonic North American Raptor Monitoring Strategy will hopefully rapidly become the American Raptor Monitoring Strategy so that it can be "exported" to all of the Western Hemisphere. It quickly became clear from that workshop that there is much information about basic owl vocalizations that is yet to be learned and/or yet to be added to nocturnal owl population monitoring.

And what about research that deals with those species that are more commonly known? These are species that are more commonly known because they more closely share "man's" environment. Because of that fact we must know much more about them.

There is always the problem, when you start citing individual works that you will leave someone's out. There are many old friends; i.e., "chronologically disadvantaged" and several new ones that fall into this category. Because of space limitations I must necessarily do this. To those whom I have not cited, my apologies. And to those whose presentations I did not hear I shall look forward to reading about your work in the Proceedings.

There is a basic triangle of research, education, and conservation that we are a part of and we need to participate in all three aspects if we are to ensure the future of the resource that has brought us together in Winnipeg; i.e., the owls. Those of you that concentrate on research are in the very best situation for educating your friends, colleagues, students, etc. and conserving the resource that you know so well.

More than once I have heard wildlife managers categorize wildlife problems as "people" problems. And often conservation problems are linked with that of technology. It does not take a genius to see what the future of this Earth, the only planet in the Universe known to contain life as we know it, will be with an ever-expanding human population and a diminishing resource base. To prevent this fate will take a global effort by people with emphasis placed on new technologies in conservation to parallel those technologies that we have developed to harvest and "consume" resources. If people and their technologies have created problems, then it will take people to resolve those problems. Who will be the people to promote these ideas? It will also take massive education efforts by many, many more Bob Neros to develop in our young people an understanding, appreciation, and willingness to conserve "our" precious resources (fig. 4) and ourselves. As Pogo has been quoted: "We have met the enemy and he is us."

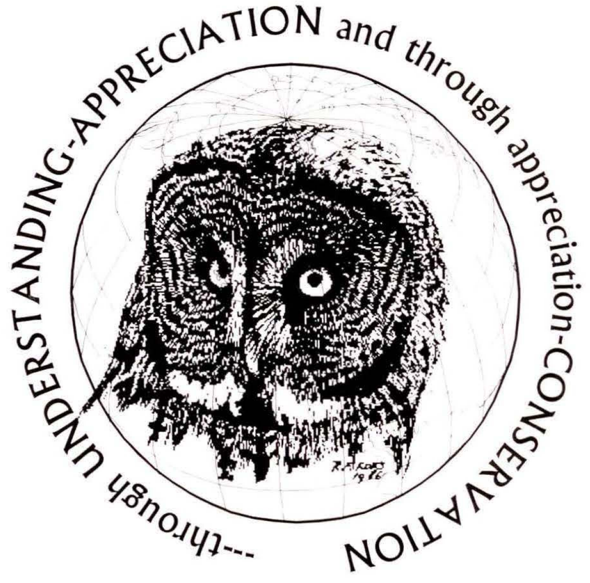
---through UNDERSTANDING-APPRECIATION and through appreciation-CONSERVATION

Figure 4.—*The "Circle of Survival" for Man and fellow creatures of the spaceship Earth.*

ACKNOWLEDGMENTS

I would like to thank the Symposium Committee for inviting me to return and the honor of summing up the Conference. Thanks also to Bob Nero and Jim Duncan for spearheading this event and for courtesies extended. Last but not least thanks to my wife Joanie who proofread the typescript for this article.

LITERATURE CITED

Brewer, R. 1994. The science of ecology. Ft. Worth, TX: Saunders College Publishing. 780 p.

Butynski, T.M.; Agenonga, U.; Ndera, B.; Hart, J.F. 1996. The world's rarest owl! Owls Magazine. 3(3): 2-4. (Published by Strix Publishing; 847A Second Avenue, Suite 247; New York, NY 10017. It reports on the mist-netting of a second individual [like the first it was thought to be a female] of *Phodilus prigoginei* in the Itombwe Forest in eastern Zaire. She was described in detail, photographed, and released.)

Enríquez Rocha, P.; Mikkola, H. 1997. Comparative study of general public owl knowledge in Central America and Africa. In: Program of the Second International Symposium: Biology and Conservation of Owls of the Northern Hemisphere; 1997 February 5-9; Winnipeg, Manitoba, Canada: 31.

Enríquez Rocha, P.; Rangel, J.L. 1997. Intra- and interspecific calling in a tropical owl community. In: Program of the Second International Symposium: Biology and Conservation of owls of the Northern Hemisphere; 1997 February 5-9; Winnipeg, Manitoba, Canada: 61.

Gerhardt, R.P; Gerhardt, D.M. 1997. Size, dimorphism, and related characteristics of *Ciccaba* owls from Guatemala. In: Program of the Second International Symposium: Biology and Conservation of owls of the Northern Hemisphere; 1997 February 5-9; Winnipeg, Manitoba, Canada: 33.

King, W.B., ed. 1981. Endangered birds of the world. ICBP Bird Red Data Book. Washington, DC: Smithsonian Institute Press.

Marcot, B.G. 1995. Owls of old forests of the world. Gen. Tech. Rep. PNW-343. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 64 p.

Mossop, D.H. 1997. The importance of old growth refugia in the Yukon boreal forest to cavity nesting owls. In: Program of the Second International Symposium: Biology and Conservation of Owls of the Northern Hemisphere; 1997 February 5-9; Winnipeg, Manitoba, Canada: 67.

Proudfoot, G.A. 1997a. Habitat use by Ferruginous Pygmy-owls in southern Texas. In: Program of the Second International Symposium: Biology and Conservation of Owls of the Northern Hemisphere; 1997 February 5-9; Winnipeg, Manitoba, Canada: 45.

Proudfoot, G.A. 1997b. Food habits of nesting Ferruginous Pygmy-owls in southern Texas. In: Program of the Second International Symposium: Biology and Conservation of Owls of the Northern Hemisphere; 1997 February 5-9; Winnipeg, Manitoba, Canada: 45.

Severinghaus, L.L. 1989. The status and conservation of Lanyu Scops Owl *Otus elegans botelsis*. In: Raptors in the modern world: proceedings of the 3d World conference on birds of prey and owls; 1987 March 22-27; Eilat, Israel: 423-431.

Sibley, C.G. 1996. Birds of the world. Version 2.0. A computerized book available in either MacIntosh or PC format from Thayer Birding Software, P.O. Box 43243, Cincinnati, OH 45243 USA

Takats, D.L.; Holroyd, G.L.; Beck, J.A. 1997. Barred owl habitat use and distribution in the Foothills Model Forest. In: Program of the Second International Symposium: Biology and Conservation of Owls of the Northern Hemisphere; 1997 February 5-9; Winnipeg, Manitoba, Canada: 71.

APPENDIX

Owls of the World According to Sibley's Birds of the World (1996), Version 2.0

A. Owl Species confined to the Northern Hemisphere

Minahassa Masked-owl (*Tyto inexspectata*)
Cape Verde Barn Owl (*Tyto detorta*)
Ashy-faced Owl (*Tyto glaucops*)

White-fronted Scops-owl (*Otus sagittatus*)
Andaman Scops-owl (*Otus balli*)
Simeulue Scops-owl (*Otus umbra*)
Luzon Scops-owl (*Otus longicornis*)
Mindoro Scops-owl (*Otus mindorensis*)
Mindanao Scops-owl (*Otus mirus*)
Sao Tome Scops-owl (*Otus hartlaubi*)
Pallid Scops-owl (*Otus brucei*)
Flammulated Owl (*Otus flammeolus*)
Oriental Scops-owl (*Otus sunia*)
Elegant Scops-owl (*Otus elegans*)
Mantanani Scops-owl (*Otus mantananensis*)
Collared Scops-owl (*Otus lettia*)
Japanese Scops-owl (*Otus semitorques*)
Mentawai Scops-owl (*Otus mentawi*)
Palawan Scops-owl (*Otus fuliginosus*)
Philippine Scops-owl (*Otus megalotis*)
Western Screech-owl (*Otus kennicottii*)
Balsas Screech-owl (*Otus seductus*)
Pacific Screech-owl (*Otus cooperi*)
Oaxaca Screech-owl (*Otus lambi*)
Eastern Screech-owl (*Otus asio*)
Whiskered Screech-owl (*Otus trichopsis*)
Bare-shanked Screech-owl (*Otus clarkii*)
Bearded Screech-owl (*Otus barbarus*)
Vermiculated Screech-owl (*Otus vermiculatus*)
Bare-legged Owl or Cuban Screech-owl (*Otus lawrencii*)
Puerto Rican Screech-owl (*Otus nudipes*)

Lesser Eagle-owl (*Mimizuku gurneyi*)

Eurasian Eagle-owl (*Bubo bubo*)
Rock Eagle-owl (*Bubo bengalensis*)
Pharaoh Eagle-owl (*Bubo ascalaphus*)
Spot-bellied Eagle-owl (*Bubo nipalensis*)
Shelley's Eagle-owl (*Bubo shelleyi*)
Dusky Eagle-owl (*Bubo coromandus*)
Philippine Eagle-owl (*Bubo philippensis*)

Blakiston's Fish-owl (*Ketupa blakistoni*)
Brown Fish-owl (*Ketupa zeylonensis*)
Tawny Fish-owl (*Ketupa flavipes*)

Snowy Owl (*Nyctea scandiaca*)

Rufous Fishing-owl (*Scotopelia ussheri*)

Spotted Wood-owl (*Strix seloputo*)
Mottled Wood-owl (*Strix occellata*)
Tawny Owl (*Strix aluco*)
Hume's Owl (*Strix butleri*)
Spotted Owl (*Strix occidentalis*)
Barred Owl (*Strix varia*)
Fulvous Owl (*Strix fulvescens*)
Ural Owl (*Strix uralensis*)
Sichuan Wood-owl (*Strix davidi*)
Great Gray Owl (*Strix nebulosa*)

Northern Hawk Owl (*Surnia ulula*)

Northern Pygmy-owl (*Glaucidium californicum*)
Mountain Pygmy-owl (*Glaucidium gnoma*)
Central American Pygmy-owl (*Glaucidium griseiceps*)
Colima Pygmy-owl (*Glaucidium palmarum*)
Tamaulipas Pygmy-owl (*Glaucidium sanchezi*)
Cuban Pygmy-owl (*Glaucidium siju*)
Eurasian Pygmy-owl (*Glaucidium passerinum*)
Collared Owlet (*Glaucidium brodiei*)
Guatemalan Pygmy-owl (*Glaucidium cobanense*)
Cape Pygmy-owl (*Glaucidium hoskinsii*)
Jungle Owlet (*Glaucidium radiatum*)
Chestnut-backed Owlet (*Glaucidium castanonotum*)
Chestnut Owlet (*Glaucidium castaneum*)

Elf Owl (*Micrathene whitneyi*)

Little Owl (*Athene noctua*)
Spotted Owlet (*Athene brama*)
Forest Owlet (*Athene blewitti*)

Boreal (Tengmalm's) Owl (*Aegolius funereus*)
Northern Saw-whet Owl (*Aegolius acadicus*)
Unspotted Saw-whet Owl (*Aegolius ridgwayi*)

Andaman Boobook (*Ninox affinis*)
Philippine Boobook (*Ninox philippensis*)

Jamaican Owl (*Pseudoscops grammicus*)

B. Owl Species confined to the Southern Hemisphere

Greater Sooty-owl (*Tyto tenebricosa*)
Lesser Sooty-owl (*Tyto multipunctata*)
Taliabu Masked-owl (*Tyto nigrobrunnea*)
Lesser Masked-owl (*Tyto sororcula*)
Manus Masked-owl (*Tyto manusi*)
Bismarck Masked-owl (*Tyto aurantia*)
Australian Masked-owl (*Tyto novaehollandiae*)
Tasmanian Masked-owl (*Tyto castanops*)
Madagascar Red Owl (*Tyto soumagnei*)
African Grass-owl (*Tyto capensis*)
Congo Bay-owl (*Phodilus prigoginei*)
Sokoke Scops-owl (*Otus ireneae*)
Beccari's Scops-owl (*Otus beccarii*)
Flores Scops-owl (*Otus alfredi*)
Enggano Scops-owl (*Otus enganensis*)
Seychelles Scops-owl (*Otus insularis*)
Malagasy Scops-owl (*Otus rutilus*)
Pemba Scops-owl (*Otus pembaensis*)
Anjouan Scops-owl (*Otus capnodes*)
Comoro Scops-owl (*Otus pauliani*)
Wallace's Scops-owl (*Otus silvicola*)
Koepcke's Screech-owl (*Otus koepckeae*)
West Peruvian Screech-owl (*Otus roboratus*)
Cloud-forest Screech-owl (*Otus huberi*)
Austral Screech-owl (*Otus usta*)
Variable Screech-owl (*Otus atricapillus*)
Hoy's Screech-owl (*Otus hoyi*)
Long-tufted Screech-owl (*Otus sanctaecatarinae*)
Palau Owl (*Otus podarginus*)
Usambara Eagle-owl (*Bubo vosseleri*)
Rusty-barred Owl (*Strix hylophila*)
Rufous-legged Owl (*Strix rufipes*)

Tawny-browed Owl (*Pulsatrix koeniswaldiana*)

Yungas Pygmy-owl (*Glaucidium bolivianum*)
Subtropical Pygmy-owl (*Glaucidium parkeri*)
Peruvian Pygmy-owl (*Glaucidium peruanum*)
Austral Pygmy-owl (*Glaucidium nanum*)
Tucuman Pygmy-owl (*Glaucidium tucumanum*)
Javan Owlet (*Glaucidium castanopterum*)
African Barred Owlet (*Glaucidium capense*)
Ngami Owlet (*Glaucidium ngamiense*)
Albertine Owlet (*Glaucidium albertinum*)

Long-whiskered Owlet (*Xenoglaux loweryi*)

Rufous Owl (*Ninox rufa*)
Powerful Owl (*Ninox strenua*)
Barking Owl (*Ninox connivens*)
Sumba Boobook (*Ninox rudolfi*)
Southern Boobook (*Ninox boobook*)
Morepork (*Ninox novaeseelandiae*)
White-browed Boobook (*Ninox superciliaris*)
Moluccan Boobook (*Ninox squamipila*)
Christmas Boobook (*Ninox natalis*)
Jungle Boobook (*Ninox theomacha*)
Manus Boobook (*Ninox meeki*)
Bismarck Boobook (*Ninox variegata*)
Russet Boobook (*Ninox odiosa*)
Solomon Islands Boobook (*Ninox jacquinoti*)

Papuan Boobook (*Uroglaux dimorpha*)

Laughing Owl (*Sceloglaux albifacies*)

Madagascar Owl (*Asio madagascariensis*)

Fearful Owl (*Nesasio solomonensis*)

C. Owl Species found in both the Northern and Southern Hemispheres

Sulawesi Owl (*Tyto rosenbergii*)
Barn Owl (*Tyto alba*)
Eastern Grass-owl (*Tyto longimembris*)

Oriental Bay Owl (*Phodilus badius*)

Reddish Scops-owl (*Otus rufescens*)
Sandy Scops-owl (*Otus icterorhynchus*)
Mountain Scops-owl (*Otus spilocephalus*)
Javan Scops-owl (*Otus angelinae*)
Sulawesi Scops-owl (*Otus manadensis*)
Common Scops-owl (*Otus scops*)
African Scops-owl (*Otus senegalensis*)
Moluccan Scops-owl (*Otus magicus*)
Rajah Scops-owl (*Otus brookii*)
Indian Scops-owl (*Otus bakkamoena*)
Sunda Scops-owl (*Otus lempiji*)
White-faced Scops-owl (*Otus leucotis*)
Tropical Screech-owl (*Otus choliba*)
Rufescent Screech-owl (*Otus ingens*)
Tawny-bellied Screech-owl (*Otus watsonii*)
Middle American Screech-owl (*Otus guatemalae*)
White-throated Screech-owl (*Otus albogularis*)

Great Horned Owl (*Bubo virginianus*)
Cape Eagle-owl (*Bubo capensis*)
Spotted Eagle-owl (*Bubo africanus*)
Fraser's Eagle-owl (*Bubo poensis*)
Barred Eagle-owl (*Bubo sumatranus*)
Verreaux's Eagle-owl (*Bubo lacteus*)
Akun Eagle-owl (*Bubo leucostictus*)

Buffy Fish-owl (*Ketupa ketupu*)

Pel's Fishing-owl (*Scotopelia peli*)
Vermiculated Fishing-owl (*Scotopelia bouvieri*)

Brown Wood-owl (*Strix leptogrammica*)
Mottled Owl (*Strix virgata*)
Black-and-white Owl (*Strix nigrolineata*)
Black-banded Owl (*Strix huhula*)
Rufous-banded Owl (*Strix albitarsus*)
African Wood-owl (*Strix woodfordii*)

Maned Owl (*Jubula lettii*)

Crested Owl (*Lophostrix cristata*)

Spectacled Owl (*Pulsatrix perspicillata*)
Band-bellied Owl (*Pulsatrix melanota*)

Andean Pygmy-owl (*Glaucidium jardinii*)
Hardy's Pygmy-owl (*Glaucidium hardyi*)
Brazilian Pygmy-owl (*Glaucidium minutissimum*)
Ferruginous Pygmy-owl (*Glaucidium brasilianum*)
Pearl-spotted Owlet (*Glaucidium perlatum*)
Red-chested Owlet (*Glaucidium tephronotum*)
Sjostedt's Owlet (*Glaucidium sjöstedti*)
Asian Barred Owlet (*Glaucidium cuculoïdes*)
Scheffler's Owlet (*Glaucidium scheffleri*)

Burrowing Owl (*Speotyto cunicularia*)

Buff-fronted Owl (*Aegolius harrisii*)

Brown Boobook (*Ninox scutulata*)
Ochre-bellied Boobook (*Ninox ochracea*)
Speckled Boobook (*Ninox punctulata*)

Stygian Owl (*Asio stygius*)
Long-eared Owl (*Asio otus*)
Abyssinian Owl (*Asio abyssinicus*)
Striped Owl (*Asio clamator*)

The Hunting Behavior of Eastern Screech-owls (*Otus asio*)

Carlo M. Abbruzzese[1] and Gary Ritchison[2]

Abstract.—We studied the nocturnal hunting behavior of eight radio-tagged Eastern Screech-owls (*Otus asio*; five females and three males) during the period from November 1994 through March 1995. Screech-owls selected low perches when hunting ($\bar{x}$ = 1.66 m), presumably to obtain a clear view of the ground and an unobstructed flight path to prey. Low perches may also improve the ability of screech-owls to hear and locate prey. Screech-owls used perches at different heights when hunting different types of prey and also tended to perch higher when moonlight was available, perhaps because increased light levels permit owls to rely more on vision. Only 8 of 35 attacks were successful, and this low success rate suggests that owls were more often attempting to capture small mammals rather than invertebrates. Male and female screech-owls exhibited similar hunting behavior, with no differences observed in the types of prey hunted or in giving up times. Weather conditions and season (early winter vs. late winter) had little effect on the hunting behavior of screech-owls.

While the hunting behavior of diurnal predators has been studied by several investigators (e.g., Fitzpatrick 1981, Greig-Smith 1983, Rice 1983, Sonerud 1992), few studies of the hunting behavior of nocturnal predators have been conducted (Bye *et al.* 1992). The hunting behavior of owls, in particular, is little known, with most information anecdotal or speculative (Bent 1938, Voous 1989). Consequently, little is known about how factors such as weather, moon phase (i.e., light levels), snow cover, sex, and temporal distribution of prey might influence the hunting habits of owls.

Eastern Screech-owls (*Otus asio*) are small, nocturnal predators found throughout eastern North America (Johnsgard 1988). Researchers have examined several aspects of their behavior and ecology, including food habits (Craighead and Craighead 1956, Ritchison and Cavanagh 1992), home range sizes and habitat use (Belthoff *et al.* 1993, Sparks *et al.* 1994), nest site selection (Belthoff and Ritchison 1990), and the postfledging behavior of adults and young (Belthoff 1987). Very little is known, however, about their hunting behavior. Gehlbach (1994) gathered information concerning the hunting behavior of Eastern Screech-owls in central Texas, however, observations were made only in suburban yards and in the immediate vicinity of nests. Thus, little is known about how screech-owls hunt in more natural habitats and at locations some distance from nest sites.

Eastern Screech-owls apparently hunt in a sit-and-wait fashion, using short flights to capture prey (Marshall 1967, Gehlbach 1994). It has also been suggested that Eastern Screech-owls may rely primarily on sight when searching for prey because they have symmetrical ear openings (Marshall 1967, Norberg 1987). Bye *et al.* (1992) suggested that Boreal Owls (*Aegolius funereus*) used low perches while hunting because they rely primarily on their sense of hearing. Thus, at least in Boreal Owls, sensory capabilities may play an important role in determining how prey are located and captured. This may also be the case for Eastern Screech-owls.

The objective of this study was to describe the hunting behavior of Eastern Screech-owls during the non-breeding period. We specifically sought to examine: (1) possible differences between the hunting behavior of males and females, (2) seasonal and temporal variation in screech-owl hunting behavior, and (3) the possible effects of weather and moon phase on hunting behavior.

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STUDY AREA

The hunting behavior of Screech-owls was studied from November 1994 through March 1995 at the Central Kentucky Wildlife Management Area, located 17 km southeast of Richmond, Madison County, Kentucky. The study area was composed of a patchwork of small deciduous woodlots, old fields, agricultural fields, and mowed fields connected by woodrows. Dominant woodland canopy tree species included shagbark hickory (*Carya ovata*), bitternut hickory (*C. cordiformis*), post oak (*Quercus stellata*), chinquapin oak (*Q. prinoides*), boxelder (*Acer negundo*), and red oak (*Q. borealis*). The mid-story layer was composed primarily of red maple (*Acer rubra*), flowering dogwood (*Cornus florida*), pawpaw (*Asiminia triloba*), spice bush (*Lindera benzoin*), silky dogwood (*C. amomum*), and hackberry (*Celtis occidentalis*). Common edge and old field tree species included black locust (*Robinia pseudo-acacia*), white ash (*Fraxinus americana*), smooth sumac (*Rhus glabra*), and sweetgum (*Liquidambar styraciflua*); while American sycamore (*Plantanus occidentalis*) and black willow (*Salix nigra*) were frequently found in wet and riparian areas. The eastern red cedar (*Juniperous virginiana*) was widely distributed throughout the study area. Two vines, summer grape (*Vitus aestivalis*) and heart-leaf ampelopsis (*Ampelopsis cordata*), were common in woodlots.

Terrestrial crayfish (*Cambarus* spp.) are common throughout much of the study area, particularly in low, poorly drained areas and along streams (Ritchison and Cavanagh 1992, pers. observ.). These crayfish typically produce small mounds of soil around the entrances to their burrows, and these mounds clearly indicate the presence of active crayfish. Other prey species that are potentially available to screech-owls in our study area include various small mammals, birds, and invertebrates (Ritchison and Cavanagh 1992).

METHODS AND MATERIALS

Beginning in November 1994, Eastern Screech-owls were captured by checking nest boxes distributed throughout the study area. Nest boxes were checked during daylight hours when screech-owls are typically docile and more easily handled. After capture, radio-transmitters (Wildlife Materials, Inc., Carbondale, IL) were attached backpack style (Smith and Gilbert 1981). Transmitters weighed approximately 6 g (3 to 4 percent of total body mass). The owls appeared to adjust quickly to the transmitters, and did not appear to behave abnormally (pers. observ.). Owls were allowed at least 1 week to become accustomed to the transmitter before observations began. To facilitate observations, a 5 to 6 cm piece of reflective tape was attached to the transmitter antennas.

Observations typically began shortly after sunset and continued for 3 to 5 hours. During owl observations, the general location of a radio-tagged owl was determined using a receiver (TR-2; Telonics, Inc., Mesa, AZ) and a hand-held, two-element antenna. Then, a Petzel headlamp or portable wheat lamp was used to scan the area from which the signal originated. Normally the light would strike the reflective tape on the transmitter's antenna and permit us to precisely locate the owl. While observing an owl, a light with a red cellophane filter was used to minimize disturbance as owls are known to have limited vision at the red end of the light spectrum (greater than 600 nm; Martin *et al.* 1975).

Eastern Screech-owls are relatively tame and typically do not fly until an observer comes within 3 or 4 m (pers. observ.). Our observations of screech-owls were usually made at a distance of 10 to 12 m using 10 x 25 binoculars. At this distance, our presence appeared to have little effect on the owls. The owls sometimes allowed us to watch them for more than an hour before moving, and owls often flew in our direction or directly over us when changing perches.

To examine possible differences in hunting behavior over time, November and December were categorized as early winter, and January, February, and March as late winter. For each hunting observation, we recorded the time the owl landed on a perch and the time until the owl either initiated an attack or left for another perch (i.e., giving up time). If an owl was not observed landing on a perch, we sometimes estimated their time of arrival at the perch by monitoring the transmitter's signal. Transmitters had activity switches so pulse rates typically changed when an owl stopped moving.

After the owl moved to another location, perches and attack sites (the point on the ground where the owl hit or attempted to hit the prey) were marked with flagging and plotted on an aerial photograph of the study area. We returned to these marked perch sites during daylight hours to measure perch heights, identify and measure the tree, shrub, or vine in which the perch was located, measure attack distances (the distance from the perch to the prey item attacked), and measure distances between consecutive perches.

We also noted whether or not attacks were successful and, if so, attempted to identify the prey species. We noted and flagged the search area (where the focal owl appeared to be looking for prey). For perches where no attack was made or where the attack was unsuccessful, we noted the type of prey (e.g., crayfish, small mammal, or bird) that the owl was probably hunting. We made this judgement based either on where the owl appeared to be searching or, less frequently, on prey species that we actually observed the owl to be watching. For example, an owl searching the ground in a low, poorly drained area with numerous crayfish burrows was assumed to be hunting crayfish, while an owl searching the ground in a drier area with no crayfish burrows was assumed to be hunting small mammals. Owls peering intently into eastern red cedars or dense shrubs were thought to be hunting birds.

During each observation period, we recorded the air temperature and, for subsequent analysis, categorized temperature as either above freezing or below freezing. We also noted the presence or absence of precipitation and, on that basis, categorized conditions as: snowing, raining, or no precipitation. We also noted the presence or absence of snow cover and whether or not the moon was visible.

Analysis

Because the number of observations on each owl varied, and to avoid bias from pooling such data (Leger and Didrichsons 1994), overall mean values were calculated using the means for each bird. We used different subsets of the data for other analyses. Owls were included in a particular analysis only if represented in all categories. For example, an owl would be included in an analysis of possible differences in perch height with season only if observed hunting during both seasons (early winter and late winter).

Multiple comparisons were made using nonparametric analysis of variance (analysis of variance on ranked data which is equivalent to the Kruskal-Wallis test; SAS Institute 1989). Paired comparisons (e.g., males versus females) were made using Wilcoxon rank sum tests (which are equivalent to Mann-Whitney U tests; SAS Institute 1989). All analyses were performed using the Statistical Analysis System (SAS Institute 1989). All values are presented as mean ± standard deviation.

RESULTS

Capture and Observation of Owls

Eight adult Eastern Screech-owls (five females and three males) were tracked during the period between November 10, 1994 and March 11, 1995. These owls were observed for a total of 168.5 hours during 91 evenings. Hereafter, these owls will be referred to by the last three digits of their U.S. Fish and Wildlife Service aluminum bands (table 1). Based on observations during previous breeding seasons and during the breeding season that followed our study, it was determined that two of these owls (male 099 and female 285) represented a mated pair. The mated status of the other owls was unknown. One owl (female 285) died during the study, and the cause of death could not be determined.

Table 1.—*Tracking period and number of nights tracked for each Eastern Screech-owl.*

Owl	Sex	Tracking period	Number of nights tracked
931	Female	11/10/94 - 2/24/95	19
016	Female	1/4/95 - 3/5/95	8
285	Female	11/14/94 - 11/24/94	4
959	Female	1/8/95 - 2/22/95	9
041	Female	11/18/94 - 2/25/95	13
099	Male	11/10/94 - 3/11/95	11
307	Male	11/11/94 - 3/8/95	14
215	Male	11/12/94 - 3/2/95	13

Hunting Behavior - Overall

Eastern Screech-owls (N = 8) used a total of 338 hunting perches, and these perches were an average of 1.66 ± 0.22 m high. The mean height of the vegetation (e.g., tree, shrub, or vine) in which these perches were located was 5.04 ± 1.81 m, and the mean d.b.h. was 11.07 ± 6.13 cm. Most hunting perches (63.2 percent) were on an open branch (25 cm or more away from the trunk), rather than near the trunk (less than 25 cm from the trunk) (23.0 percent) or on the stub or top of a plant (13.8 percent).

Owls (N = 6) initiated 35 attacks from hunting perches, with 27 being unsuccessful (no prey captured) and eight successful. The successful attacks resulted in the capture of one bird, one crayfish, one small mammal, and five moths. The mean attack distance was 3.41 ± 0.79 m. Owls (N = 8) remained on perches for an average of 393.7 ± 204.2 sec before either attacking or giving up. Screech-owls (N = 8) leaving perches without making an attack (i.e., giving up time) remained on perches for an average of 278.9 ± 99.3 sec, while owls (N = 5) that attacked prey were on perches for an average of 226.1 ± 108.9 sec prior to initiating the attack. Mean giving up time for these latter five owls was 323.9 ± 90.4 sec. When owls (N = 6) changed perches (either after an attack or after giving up), the mean distance between consecutively used perches was 9.28 ± 4.12 m.

Screech-owls appeared to hunt six different types of prey: birds, insects, crayfish, small mammals, leeches, and fish. Owls appeared to hunt primarily crayfish (49.7 percent of all observations), small mammals (29.7 percent), and birds (5.4 percent) (fig. 1). Four owls (041, 215, 931, and 959) were observed hunting all three of these primary prey items, and perch height varied significantly with type of prey being hunted ($F_{2,9}$ = 17.69, P = 0.0008). Mean perch height when hunting birds was 2.86 ± 1.11 m. By contrast, mean perch height was 1.90 ± 0.45 m when owls were hunting small mammals and 1.27 ± 0.10 m when hunting crayfish. We found no significant differences in the perch position (open branch, near trunk, or at the top of the plant) used by owls hunting the three primary prey items (χ^2 = 6.7, df = 4, P = 0.155). Giving up times for these four owls varied significantly with type of prey hunted ($F_{2,6}$ = 6.35, P = 0.033): a mean of 308.7 ± 539.7 sec for crayfish, 486.8 ± 522.7 sec for small mammals, and 721.9 ± 1175.9 sec for birds.

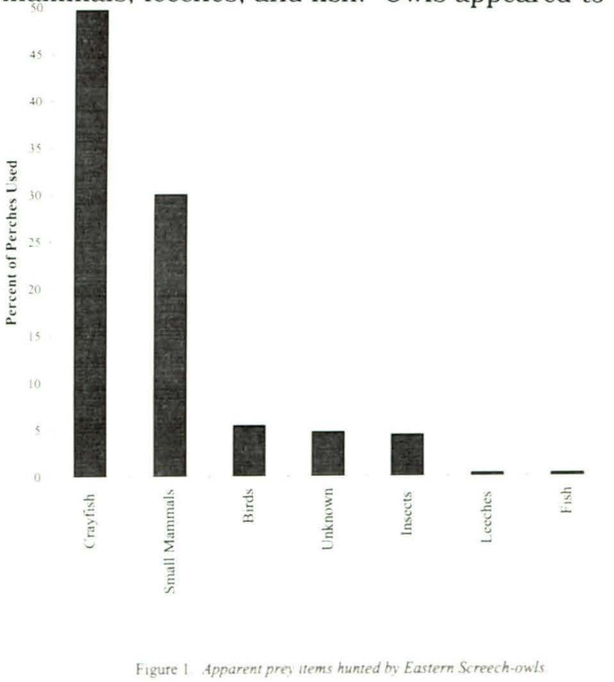

Figure 1.—*Apparent prey items hunted by Eastern Screech-owls.*

Hunting Behavior - Males versus Females

Hunting perches used by male and female screech-owls did not differ significantly in height (z = 0, P = 0.99), with a mean perch height of 1.65 ± 0.18 m for females (N = 5) and 1.66 ± 0.35 m for males (N = 3). Similarly, there were no differences in either the mean height (z = 0.89, P = 0.37; $\overline{x}$ = 5.69 ± 1.98 m for females and 3.97 ± 0.93 m for males) or mean d.b.h. (z = 1.49, P = 0.14; $\overline{x}$ = 13.56 ± 6.60 cm for females and 6.92 ± 1.70 cm for males) of the vegetation in which these perches were located. Males and females did, however, exhibit a significant difference in choice of perch positions (χ^2 = 7.6, df = 2, P = 0.023), with females more likely to perch near the trunk and males more likely to perch on the stub or top of a plant (fig. 2).

We found no difference between male and female screech-owls (z = 0.6, P = 0.55) in giving up time: a mean of 238.8 ± 122.7 sec for males (N = 3) and 303.0 ± 88.4 sec for females (N = 5).

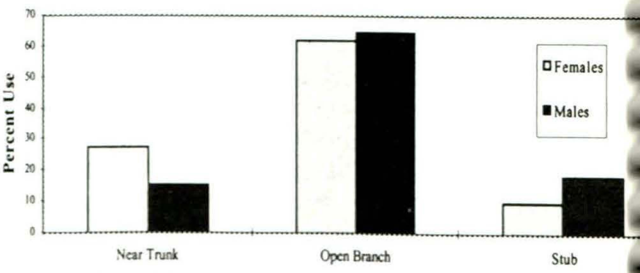

Figure 2.—*Choice of perch positions by male and female Eastern Screech-owls.*

We also found no difference (z = 0.29, P = 0.77) between males and females in mean attack time, with a mean of 273.3 ± 122.4 sec for females (N = 3) and 155.4 ± 28.4 sec for males (N = 2).

Male and female screech-owls also did not differ (z = 0, P = 0.99) in mean attack distance. The mean attack distance for females (N = 4) was 3.64 ± 0.91 m, while for males (N = 2) the mean distance was 2.96 ± 0.01 m. Similarly, the mean distance between consecutive perches did not differ (z = 0.23, P = 0.82) between the sexes, with females (N = 4) moving a mean distance of 8.3 ± 4.8 m and males (N = 2) a mean distance of 11.3 ± 2.0 m.

Both males and females appeared to hunt primarily for crayfish, followed by small mammals and birds. There was no difference (χ^2 = 1.8, df = 2, P = 0.4) between the sexes in the frequency with which they appeared to be hunting for the three primary prey items.

Hunting Behavior - Effect of Outcome

The height of hunting perches from which attacks were initiated ($\overline{x}$ = 1.54 ± 0.36 m; N = 6 owls) did not differ significantly (z = 0.8, P = 0.42) from that of perches from which owls did not initiate attacks ($\overline{x}$ = 1.59 ± 0.16 m; N = 6 owls). The mean height of perches from which successful attacks were initiated was 1.58 ± 0.59 m (N = 4 owls), while that for perches from which unsuccessful attacks were initiated was 1.40 ± 0.71 m (N = 4 owls). This difference was not significant (z = 0.43, P = 0.67). The mean attack distance was 3.10 ± 1.34 m (N = 4 owls) for successful attacks and 4.03 ± 2.31 m (N = 4 owls) for unsuccessful attacks, and this difference was not significant (z = 0.14, P = 0.89).

Screech-owls (N = 6) that eventually initiated an attack remained on perches for an average of 614.6 ± 956.5 sec, while those that did not initiate an attack remained on perches an average of 299.9 ± 100.0 sec. This difference in perch time was not significant (z = 0.56, P = 0.58). One owl (Female 285) had a longer perch time prior to attack than the other owls because she once spent 84 minutes on a perch before making an attack. It is likely that this female, while roosting, happened to locate and then attack a prey item. If female 285 is removed from the analysis, the mean time until attack decreases to 226.1 ± 108.9 sec (N = 5 owls) and the mean time until giving up increases slightly to 323.9 ± 90.4 s (N = 5 owls). Nonetheless, this difference in perch time is still not significant (z = 1.2, P = 0.21).

Hunting Behavior - Probability of Prey Detection and Pattern of Giving Up

For a screech-owl on a perch searching for a prey item, the probability of detecting prey may increase, decrease, or remain the same as time passes. As described by Bye *et al.* (1992:270): "The cumulative distribution of detection times may be used to determine which of these possibilities is the case. This distribution decays exponentially if the probability of detecting prey remains constant. If the probability of prey detection increases or decreases, this will appear as a concave or convex deviation, respectively, from the exponential model." For all screech-owls that initiated attacks, we plotted the proportion of owls still remaining on their perches versus perch time (total time spent on the perch). These proportions were log-transformed to facilitate the assessment of fit to an exponential model (Bye *et al.* 1992). The decay in the distribution of attack times (detection times) was, in fact, close to exponential (fig. 3). The straight line representing the

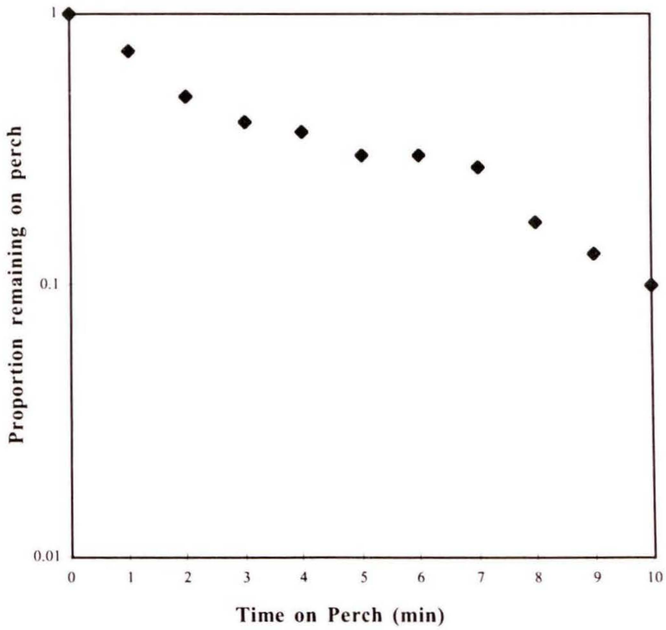

Figure 3.—*Proportion of Eastern Screech-owls remaining on perch in relation to time on perch for perches from which an attack was made (N = 35). The straight line pattern indicates that how soon an owl is likely to attack is not predicted by perch time.*

best-fitting exponential model for attack times up to 10 min was log $y = -0.09x - 0.056$. In other words, prey were attacked by screech-owls at a constant rate.

The decay in the distribution of giving-up times was also close to exponential (fig. 4). The straight line representing the best-fitting exponential model for giving-up times up to 10 min was log $y = -0.09x - 0.036$. Thus, screech-owls also gave-up at a constant rate.

Hunting Behavior - Effect of Season

Examination of the hunting behavior of owls (N = 5) observed during both early and late winter revealed no significant seasonal variation in perch height, height or d.b.h. of the vegetation in which perches were located, perch time (before either giving up or attacking), attack distance, or distance between consecutive perches (table 2).

Table 2.—*Seasonal variation in the hunting behavior of Eastern Screech-owls. (Numbers represent mean ± standard deviation.)*

	Early winter (Nov.-Dec.)	Late winter (Jan.-March)
Perch height (m)	1.65 ± 0.16	2.14 ± 0.90
Perch tree/shrub height (m)	3.93 ± 1.21	5.88 ± 3.62
Perch d.b.h. (cm)	7.84 ± 2.68	11.16 ± 10.34
Perch time (sec)	319.3 ± 155.0	368.8 ± 305.5
Attack dist. (m)	3.42 ± 0.72	3.47 ± 2.07
Interperch distance (m)	8.98 ± 4.73	9.95 ± 2.08

We also examined possible seasonal variation in the types of prey that the four most frequently observed owls appeared to be hunting. Although three of these owls exhibited significant seasonal variation (χ^2 tests, $P < 0.035$), and variation for the fourth owl approached significance ($\chi^2 = 5.45$, df = 2, $P = 0.065$), no clear trends were apparent. For example, two owls (307 and 041) appeared to be hunting for small mammals more than expected during early winter, while, in contrast, the other two owls (931 and 215) hunted for small mammals more than expected during late winter. Also illustrating the absence of any trends, one owl (931) hunted for crayfish more than expected in early winter, while two owls (307 and 041) did the same in late winter.

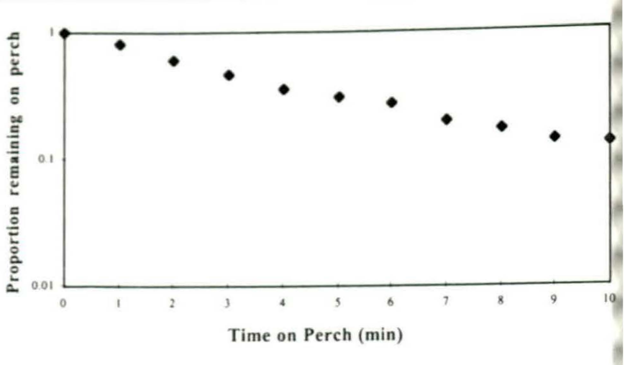

Figure 4.—*Proportion of Eastern Screech-owls remaining on perch in relation to time on perch for perches that were given up (N = 303). The straight line pattern indicates that how soon an owl is likely to give up is not predicted by perch time.*

Hunting Behavior - Effect of Moonlight and Weather

Screech-owls chose significantly higher perches when moonlight was available (i.e., 1/4 moon, 1/2 moon, 3/4 moon, or full moon) than when moonlight was not available ($z = 2.09$, $P = 0.036$), with a mean perch height of 1.88 ± 0.35 m (N = 5 owls) when moonlight was available and 1.46 ± 0.08 m (N = 5 owls) when moonlight was not available.

Three owls (016, 215, and 931) were observed hunting during all weather conditions (snowing, raining, and no precipitation) and these varying conditions had no apparent effect on the type of prey that owls hunted ($\chi^2 = 1.68$, df = 4, $P = 0.79$). Similarly, temperature (above versus below freezing) had no effect on the type of prey being hunted by Screech-owls ($\chi^2 = 4.57$, df = 2, $P = 0.102$). Screech-owls appeared to hunt for crayfish at similar rates both when air temperatures were above and below freezing. Temperature also had no significant effect on giving up times ($z = 1.46$, $P = 0.14$), with owls giving up after 366.2 ± 40.3 sec (N = 5 owls) when temperatures were above freezing and after 264.2 ± 148.4 sec (N = 5 owls) when below freezing.

Hunting Behavior - Effect of Time of Night

Overall, screech-owls exhibited significant temporal variation in type of prey hunted ($\chi^2 = 38.1$, df = 6, $P < 0.0001$), with owls more likely to hunt for crayfish early in the evening (1800 - 2300 h) and small mammals later in the evening (2300 - 0300 h). We had sufficient numbers of observations on six owls (016, 041, 215, 307, 931, and 959) to permit examination of possible temporal variation in type of prey hunted, and three of these owls (041, 215, and 959) exhibited the same significant (χ^2 tests, $P < 0.035$) tendency to hunt for crayfish earlier and small mammals later. In addition, this tendency approached significance ($\chi^2 = 9.6$, df = 6, $P = 0.14$) for another owl (931). The remaining two owls (016 and 307) appeared to hunt for crayfish and small mammals at similar levels throughout the night.

We found little evidence that giving up times varied with time of night. For five owls with sufficient number of observations for analysis (041, 215, 307, 931, and 959), only one exhibited significant temporal variation in giving up time. This female (041) had significantly shorter giving up times early in the evening ($\bar{x} = 172.1 \pm 144.8$ sec; $N = 26$) than later in the evening ($\bar{x} = 595.5 \pm 666.9$ sec; $N = 13$) ($z = 2.55$, $P = 0.011$). Three other owls (307, 931, and 959) also had shorter giving up times early in the evening, but differences in giving up times between early and late evening were not significant (Wilcoxon tests, $P > 0.09$).

DISCUSSION

Hunting Perches

The mean perch height for hunting Eastern Screech-owls in this study was 1.66 m. By contrast, screech-owls roosting on open limb perches in the same study area were found at a mean height of 10.2 m (Belthoff and Ritchison 1990). Gehlbach (1995) also reported that screech-owls used higher perches when roosting ($\bar{x} = 4$ m) than when hunting ($\bar{x} = 2.6$ m). Boreal Owls also use higher perches for roosting than for hunting (Bye *et al.* 1992). Owls may select higher perches for roosting because such sites may provide more cover than lower sites (Bye *et al.* 1992). In fact, Belthoff and Ritchison (1990) noted that screech-owls typically selected roost sites that provided concealment. The lower perch sites selected by hunting owls probably provide an unobstructed view of, and unobstructed access to, the ground (Bye *et al.* 1992), an important consideration for predators that largely depend on ground-based prey.

Screech-owls in this study used lower hunting perches than reported for other species of owls. For example, the mean height of hunting perches was found to be 3.3 m for Boreal Owls (Bye *et al.* 1992), 5.5 m for Great Gray Owls (*Strix nebulosa*; Bull and Henjum 1990), and 8.5 m for Northern Hawk Owls (*Surnia ulula*; Sonerud 1992). Norberg (1970), however, reported that the mean height of hunting perches used by Boreal Owls was 1.7 m, similar to that for screech-owls in this study. Several factors may influence the height of perches selected by hunting owls. An owl's sensory capabilities may be one such factor. For example, owls that depend heavily on acoustic cues to localize ground-dwelling prey may need to be a short distance from potential prey (Andersson 1981, Rice 1982, 1983). Thus, the use of low hunting perches by screech-owls in this study suggests that they may depend on hearing to locate prey. Anatomical evidence, however, suggests that screech-owls should be more dependent on vision. That is, screech-owls have symmetrical ears and Norberg (1987) suggested that owls with such ears may rely more on vision while those with asymmetrical ears may rely more on hearing. This may be true because asymmetrical ear openings would permit an owl to simultaneously locate prey on both the horizontal and vertical planes, but symmetrical ear openings do not preclude the use of hearing to locate prey. Owls with symmetrical ears could simply determine horizontal and vertical directions one after the other with an intervening tilting of the head (Norberg 1987). This technique would require more time but might still be effective when hunting relatively slow moving prey like terrestrial crayfish. It is likely, therefore, that screech-owls hunting from low perches may, in part, be seeking auditory cues concerning the location of prey. Other investigators have also reported observations suggesting that Eastern Screech-owls hear well and may, at times, depend on hearing to locate prey. For example, Bent (1938) and Gehlbach (1994) reported that screech-owls were able to locate prey hidden in leaf litter.

The type of prey being hunted may also influence the height of hunting perches. We found that screech-owls that appeared to be hunting crayfish perched lower than when apparently hunting small mammals or birds. Screech-owls that appeared to be hunting birds used relatively high perches, perhaps because avian prey were located in dense vegetation (e.g., cedars) rather than on the ground. Although both crayfish and small mammals are found on the ground, screech-owls perched significantly lower when apparently hunting crayfish. One reason for such behavior may be that slower moving crayfish are more difficult to detect. Similarly, Pinkowski (1977) found that Eastern Bluebirds (*Sialia sialis*) perched lower in the spring (March 15 - April 15), because "smaller, fewer, or less active" insects were more difficult to detect at greater heights. Also, crayfish and, perhaps, invertebrates (or ectotherms) in general may be less likely to detect a nearby predator (particularly during cooler weather) than would more active (and alert) small mammals.

Light levels may also influence the height of hunting perches. As already noted, Great Gray Owls and Northern Hawk Owls use relatively high hunting perches compared to screech-owls. These two species both hunt during the day when visibility is relatively high. In contrast, screech-owls are primarily nocturnal (and all our observations were made after sunset). Although screech-owls and other nocturnal owls do have eyes well-adapted for seeing under low-light conditions (Norberg 1987), they may have to perch lower to detect and accurately locate prey. Supporting this view, the hunting perches of screech-owls in this study were significantly higher when moonlight was available.

The height of hunting perches may also be influenced by perch availability. For example, screech-owls in suburban Waco, Texas, used higher hunting perches ($\bar{x}$ = 2.6 m; Gehlbach 1994) than did screech-owls in this study. One possible factor for such differences may be that the vegetation in suburban areas has been substantially altered and typically has little understory (Beissinger and Osborne 1982, Gehlbach 1994). Thus, fewer low branches may be available as perch sites for hunting screech-owls.

The hunting perches of screech-owls were primarily on open branches of small trees or shrubs and at least 25 cm from the main trunk. Such sites, in contrast to typical roost sites (Belthoff and Ritchison 1990), provided little concealment and, as a result, may increase an owl's vulnerability to predation (e.g., by Great Horned Owls, *Bubo virginianus*). As already noted, however, hunting owls must have an unobstructed view that may not be available on perches located closer to, or against, the main trunk. Perhaps in an attempt to reduce the chances of being spotted by a larger predator (as well as to reduce the chances of being spotted by potential prey), screech-owls typically remain motionless (and silent) when on hunting perches (pers. observ.).

Attack Distance and Success

The mean attack distance for screech-owls in this study was 3.41 m. Similarly, mean attack distances for Boreal Owls were reported to be 4.4 m (Norberg 1970) and 5.6 m (Bye *et al.* 1992). Bye *et al.* (1992) suggested that such relatively short attack distances indicate a restricted search area and, further, also indicate that prey are being located using acoustic cues.

Only 8 of 35 attacks (22.8 percent) by screech-owls were successful. Similarly, Ural Owls (*Strix uralensis*) hunting rodents were successful 27 percent of the time (Nishimura and Abe 1988) and Great Gray Owls also hunting rodents were successful 33 percent of the time (Bull and Henjum 1990). Eastern Screech-owls in Texas successfully captured 56 percent of vertebrate prey attacked and 83 percent of invertebrate prey attacked (Gehlbach 1994). Such results indicate that attack success rates vary with prey type, with invertebrate prey more likely to be successfully captured than vertebrate prey. The limited success of screech-owls in this study may indicate that they were attacking primarily small mammals. Whereas success rates may be higher for invertebrate prey, screech-owls may hunt small mammals because smaller invertebrates may represent less energy and, at times (e.g., during the winter months), may not be available.

Search Time

For the five screech-owls we observed both when giving up and when attacking, the mean giving up time was 323.9 sec while the mean time until attack (or detection time; Carlson 1985) was 226.1 sec. Similarly, giving up times were longer than detection times for insectivorous, or primarily insectivorous, Spotted Flycatchers (*Muscicapa striata*; Davies 1977), Eastern Bluebirds (Pinkowski 1977), and American Kestrels (*Falco sparverius*; Rudolph 1982). In contrast, detection times were found to be longer in duration than giving up times for two species of owls that prey primarily on small mammals, Boreal Owls (Bye *et al.* 1992) and Northern Hawk Owls (Sonerud 1989). Several investigators have noted that small mammals are more difficult for predators to catch than are insects (e.g., Sonerud 1980 cited in Bye *et al.* 1992, Temeles 1985). As a result, Sonerud (1989) suggested that an owl must wait longer before initiating an attack. If so, observed detection times would appear longer than actual detection times because owls are waiting for an undetermined period of time before launching an attack on already detected prey. Thus, one possible explanation for the short detection times (relative to giving up times) observed in this study is that screech-owls were hunting primarily insects and other invertebrates (i.e., crayfish). Screech-owls hunting primarily small mammals might have longer mean detection times. Unfortunately, we were unable to identify a sufficient number of prey to determine if attack times (detection times) for screech-owls varied with type of prey.

A predator attempting to optimize its hunting effort might be expected to abandon a perch as the probability of detecting prey begins to decline (Fitzpatrick 1981). However, screech-owls in this study gave up and attacked prey at a constant rate, and similar results have been reported for Boreal Owls (Bye *et al.* 1992). Fitzpatrick (1981) explained such behavior by suggesting that birds can assess the complexity of the search area around each perch independently after landing and estimate how long it will take to search it thoroughly. If a prey item appears during this time, the bird attacks and, if not, the bird gives up. If an owl's home range includes a random selection of perches with respect to the quality of search areas, the perch survivorship curve will decline exponentially (Bye *et al.* 1992).

Males versus Females

We found few differences in the hunting behavior of male and female screech-owls. Males and females did differ significantly in perch location, with males more likely to perch on the very top of plants and females more likely to perch near the trunk. This difference may be due, at least in part, to differences in body size. Female screech-owls typically weigh more than males (Gehlbach 1994, Henny and VanCamp 1979, pers. observ.) and, as a result, may have to perch on the slightly larger and stronger branches located closer to the trunk of small trees and shrubs. The similar hunting techniques of male and female screech-owls in our study may be due to similarities in the types of prey being hunted. We found that males and females appeared to hunt primarily for crayfish and small mammals. Similarly, Hofstetter (1995) reported that male and female screech-owls on the same study area captured the same types of prey during the breeding season.

Bye *et al.* (1992) found that female Boreal Owls had longer giving up times than males, and suggested that larger females should wait longer than smaller males because the cost of flight is greater for larger females. We found no difference between male and female screech-owls in giving up time. This apparent difference in the behavior of Boreal Owls and Eastern Screech-owls may be due to differences in the degree of sexual dimorphism. Female Boreal Owls are 4 percent larger than males by wing length and 64 percent larger by body mass (Korpimaki 1986, Lundberg 1986). In contrast, female screech-owls are typically only 16-17 percent larger in body mass than males (Henny and VanCamp 1979, Gehlbach 1994). As with screech-owls in this study, Bye *et al.* (1992) found that male and female Boreal Owls did not differ significantly in the mean height of hunting perches.

Moon Phase, Weather, and Season

Screech-owls in this study perched significantly higher when moonlight was available, perhaps because more light may permit hunting owls to see greater distances and, therefore, perch higher. In addition, however, more light may permit screech-owls to rely more on vision than on hearing. Because visual hunters need not be as close to prey as acoustic hunters, screech-owls relying on vision to locate prey would be able to perch higher.

Screech-owls in this study exhibited no changes in hunting behavior with season or with changing weather conditions. Our study was conducted over a 4-month period, and conditions during that limited time may not have varied sufficiently to influence prey availability or hunting behavior. Studies conducted over longer periods have revealed that the food habits of Eastern Screech-owls do vary seasonally, with more invertebrates taken during the breeding period (March-August) than during the non-breeding period (September-February; Ritchison and Cavanagh

1992). Such changes in prey use would, as observed in this study, cause corresponding changes in hunting behavior.

An important factor in the seasonal variation in prey used by screech-owls is that invertebrates are less likely to be available during colder weather (Ritchison and Cavanagh 1992). Screech-owls in our study hunted primarily for crayfish, an invertebrate whose activity (and therefore availability to screech-owls) may be influenced by temperature. If so, fewer crayfish should have been available at lower temperatures and, as a result, screech-owls should have altered their hunting behavior (perhaps, for example, by hunting for endotherms like small mammals and birds). No such change in behavior was observed. A likely explanation for this is that the crayfish hunted by screech-owls in our study apparently remained active and available as prey even when temperatures were below freezing.

Time of Night

Four of six screech-owls observed hunting both early and late in the evening exhibited a tendency to hunt for crayfish early in the evening (1800 - 2300 h) and small mammals later in the evening (2300 - 0300 h). Because crayfish are ectotherms, declining temperatures as the evening progresses might reduce crayfish activity levels and, therefore, availability. As noted previously, the crayfish on our study area apparently remain active even when temperatures are below freezing. Another possible explanation is that the availability of crayfish and small mammals varies with nightly variation in their normal activity patterns, with crayfish more active early in the evening and small mammals later in the evening. We have no information, however, concerning the normal activity patterns of these prey species.

ACKNOWLEDGMENTS

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LITERATURE CITED

Andersson M. 1981. On optimal predator search. Theoretical Population Biology. 19: 58-86.

Belthoff, J.R. 1987. Post-fledging behavior of the Eastern Screech-owl (*Otus asio*). Richmond, KY: Eastern Kentucky University. M.S. thesis.

Belthoff, J.R.; Ritchison, G. 1990. Roosting behavior of postfledging Eastern Screech-owls. Auk. 107: 567-579.

Belthoff, J.R.; Sparks, E.J.; Ritchison, G. 1993. Home ranges of adult and juvenile Eastern Screech-owls: size, seasonal variation and extent of overlap. Journal of Raptor Research. 27: 8-15.

Bent, A.C. 1938. Life histories of North American birds of prey, Part 2. Bull. 170. Washington, DC: U.S. National Museum.

Beissinger, S.R.; Osborne, D.R. 1982. Effects of urbanization on avian community organization. Condor. 84: 74-83.

Bull, E.L.; Henjum, M.G. 1990. Ecology of the Great Gray Owl. Gen. Tech. Rep. GTR-PNW-265. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station.

Bye, F.N.; Jacobsen, B.V.; Sonerud, G.A. 1992. Auditory prey location in a pause-travel predator: search height, search time, and attack range of Tengmalm's Owls (*Aegolius funereus*). Behavioral Ecology. 3: 266-276.

Carlson, A. 1985. Prey detection in the Red-backed Shrike (*Lanius collurio*): an experimental study. Animal Behavior. 33: 1243-1249.

Craighead, J.J.; Craighead, F.C., Jr. 1956. Hawks, owls, and wildlife. Harrisburg, PA: Stackpole Co.

Davies, N.B. 1977. Prey selection and the search strategy of the Spotted Flycatcher (*Muscicapa striata*): a field study on optimal foraging. Animal Behavior. 25: 1016-1033.

Fitzpatrick, J.W. 1981. Search strategies of tyrant flycatchers. Animal Behavior. 29: 810-821.

Gehlbach, F.R. 1994. The Eastern Screech-owl: life history, ecology, and behavior in suburbia and the countryside. College Station, TX: Texas A&M University Press.

Gehlbach, F.R. 1995. Eastern Screech-owl (*Otus asio*). In: Poole, A.; Gill, F., eds. The birds of North America. No.165. Philadelphia, PA: The Academy of Natural Sciences, and Washington, DC: The American Ornithologists' Union.

Greig-Smith, P.W. 1983. Use of perches as vantage points during foraging by male and female Stonechats, *Saxicola torquata*. Behaviour. 86: 215-236.

Henny, C.J.; Van Camp, L.F. 1979. Annual weight cycle in wild screech owls. Auk. 96: 795-796.

Hofstetter, S.H. 1995. The provisioning behavior of adult Eastern Screech-owls: prey use, sex differences, and the effect of nestling behavior. Richmond, KY: Eastern Kentucky University. M.S. thesis.

Johnsgard, P.A. 1988. North American owls: biology and natural history. Washington, DC: Smithsonian Institution Press.

Korpimaki, E. 1986. Reversed size dimorphism in birds of prey, especially in Tengmalm's Owl *Aegolius funereus*: a test of the "starvation hypothesis." Ornis Scandinavica. 17: 326-332.

Leger, D.W.; Didrichsons, I.A. 1994. An assessment of data pooling and some alternatives. Animal Behavior. 48: 823-832.

Lundberg, A. 1986. Adaptive advantages of reversed sexual dimorphism in European owls. Ornis Scandinavica. 17: 133-140.

Marshall, J.T., Jr. 1967. Parallel variation in North and Middle American screech owls. Western Foundation of Vertibrate Zoology Monograph. 1: 1-72.

Martin, G.R.; Gordon, I.E.; Cadle, D.R. 1975. Electroretinographically determined spectral sensitivity in the Tawny Owl (*Strix aluco*). Journal of Comparative Physiological Psychology. 89: 72-78.

Nishimura, K.; Abe, M.T. 1988. Prey susceptibilities, prey utilization and variable attack efficiencies of Ural Owls. Oecologia. 77: 414-33.

Norberg, R.A. 1970. Hunting technique of Tengmalm's Owl *Aegolius funereus*. Ornis Scandinavica. 1: 51-64.

Norberg, R.A. 1987. Evolution, structure, and ecology of northern forest owls. In: Nero, R.W.; Clark, R.J.; Knapton, R.J.; Hamre, R.H., eds. Biology and conservation of Northern Forest Owls. Gen. Tech. Rep. RM-142. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station.

Pinkowski, B.C. 1977. Foraging behavior of the Eastern Bluebird. Wilson Bulletin. 89: 404-414.

Rice, W.R. 1982. Acoustical location of prey by the Marsh Hawk: adaptation to concealed prey. Auk. 99: 403-413.

Rice, W.R. 1983. Sensory modality: an example of its effect on optimal foraging behavior. Ecology. 64: 403-406.

Ritchison, G.; Cavanagh, P.M. 1992. Prey use by Eastern Screech-owls: seasonal variation in central Kentucky and a review of previous studies. Journal of Raptor Research. 26: 66-73.

Rudolph, S.G. 1982. Foraging strategies of American Kestrels during breeding. Ecology. 63: 1268-1273.

SAS Institute. 1989. SAS user's guide: statistics. 1989 ed. Cary, NC: SAS Institute.

Smith, D.G.; Gilbert, R. 1981. Backpack radio transmitter attachment success in Screech Owls (*Otus asio*). North American Bird Bander. 6: 142-143.

Sonerud, G.A. 1980. Jaktstrategier hos flyvende smapattedyr predatorer i barskog. Cand. Oslo, Norway: University of Oslo. Cand. real. thesis.

Sonerud, G.A. 1989. Search strategies of predators and avoidance strategies of prey, illustrated by birds and mammals in the boreal ecosystem of Fennoscandia. Oslo, Norway: University of Oslo. Ph.D. dissertation.

Sonerud, G.A. 1992. Search tactics of a pause-travel predator: adaptive adjustments of perching times and move distances by Hawk Owls, *Surnia ulula.* Behavioral Ecology and Sociobiology. 30: 207-217.

Sparks, E.J.; Belthoff, J.R.; Ritchison, G. 1994. Habitat use by Eastern Screech-owls in central Kentucky. Journal of Field Ornithology. 65: 83-95.

Temeles, E.J. 1985. Sexual size dimorphism of bird-eating hawks: the effects of prey vulnerability. American Naturalist. 125: 485-499.

Voous, K.H. 1989. Owls of the northern hemisphere. Cambridge, MA: M.I.T. Press.

Albinism in the Great Gray Owl (*Strix nebulosa*) and Other Owls

Pentti Alaja and Heimo Mikkola[1]

Abstract.—An incomplete albino Great Gray Owl (*Strix nebulosa*) was observed in Vesanto and Kajaani, Finland, 1994-1995. The literature pertaining to albinism in owls indicates that total and incomplete albinism has only been reported in 13 different owl species, the Great Gray Owl being the only species with more than five records. Thus six to seven incomplete albino Great Grays have been recorded since 1980 in Canada, Finland, and the United States.

It would seem that most animals produce occasional albinos; some species do so quite frequently whilst this phenomenon is much rarer in others. Although albinism in most avian families is frequently recorded, we know of very few abnormally white owls. Thus the motive of this paper is to assemble as complete a record as possible of white or light color mutations of owls which exist or have been recorded.

GENETICS OF ALBINISM

Albinism is derived from a recessive gene which inhibits the enzyme tyrosinase. Tyrosine, an amino acid, synthesizes the melanin that is the basis of many avian colors (Holt *et al.* 1995). Albinism in birds has been separated into four categories:

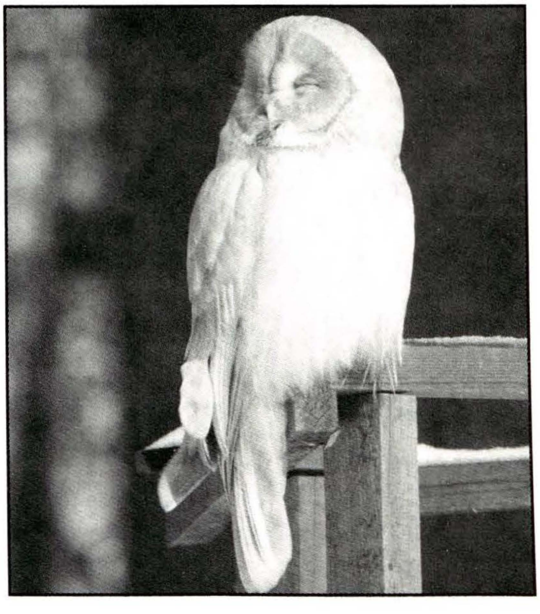
1. Total albinism—a simultaneous complete absence of melanin from the eyes, skin, and feathers. This is the rarest form. Gross (1965) reported 7 percent of 1,847 cases of avian albinism examined as being of this type.
2. Incomplete albinism—when melanin is not simultaneously absent from the eyes, skin, and feathers.
3. Imperfect albinism—when melanin is reduced in the eyes, skin, and feathers; and
4. Partial albinism—when albinism is localized to certain areas of the body (Mueller and Hutt 1941).

Partial albinism may result from injury, physiological disorder, diet, or circulatory problems. This type of albinism is most frequently observed. It is important to note that white plumage is not necessarily proof of albinism.

Adult Snowy Owls (*Nyctea scandiaca*) are primarily white, but have their feather color derived from a schemochrome feather structure which possesses little or no pigment. Light reflects within the feather structure and produces the white coloration (Holt *et al.* 1995).

ALBINISM IN THE GREAT GRAY OWLS

An extremely light and large Great Gray Owl was first seen on March 27, 1994 in Vesanto,



Pentti Alaja

Incomplete Albino Great Grey Owl in Vesanto, Finland, 1994.

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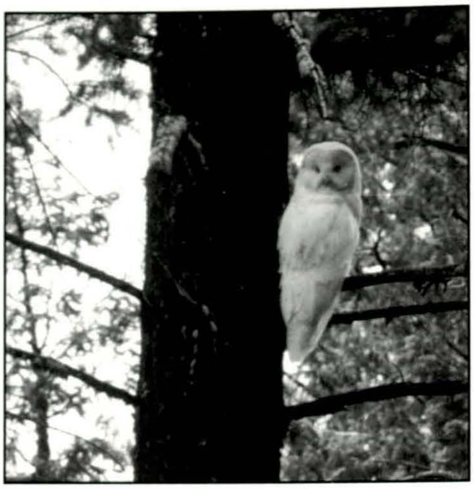
central Finland, where a great invasion of the great grays was witnessed in that spring. Six 'normal' Great Gray Owls were seen in March - April in a pasture area of about 20 ha. Due to the poor prey (vole) situation no known breeding took place in 1994 despite active courtship observed between the light and a normal great gray in the area. The last observation of the light and large owl was made in November 1994 about 2 km away from the field. After that, no great grays have been seen in the area to date (1996).

In 1995, a similar large and white Great Gray Owl was again seen in March, near Kajaani, about 165 km north from Vesanto (P. Helo, pers. comm.). By comparing the photos taken by Pentti Alaja and Pekka Helo of both birds, they were thought to be the same individual.

The crown, nape, mantle, scapulars, back, breast, flanks, and belly of the light owl were almost white. The ruff and facial disc lacked the barring and the typical great gray's concentric circles were not visible, although the face and edge of the ruff had some light brown markings. The eyes, however, were yellow, edged on the inside with a touch of blackish-brown. Two large outward-facing 'commas' were white as usual. The bill was normal, but surrounded by a brown 'beard' instead of the normal black. The owl had white 'moustaches' and fairly prominent white patches in the middle of the foreneck as usual. Flight and tail feathers were also very light, but had some faint brown markings giving the bird a somewhat yellowish look. Also, the toes, talons, and tarsus were much lighter than normal.

Although this owl was very light, we conclude it best fits the incomplete albino definition, as its eyes and toes were not pink. Other reports of the same bird listed it as an albino (Wanders 1994) or as leucistic (Lehto and Lehto 1995). Leucistic means birds with muted coloration.

In the United States, the first imperfect Great Gray Owls were seen in 1980 by Mary Maj on the Targhee National Forest, Idaho. Between 1990 and 1992 several observations of an adult white Great Gray Owl were recorded in southeastern Idaho, some 112 km from the Targhee National Forest site. This owl was more strikingly white than the one(s) seen by Maj (Whitfield *et al.* 1995), i.e., it was the first incomplete albino reported in the United States.


Michael B. Whitfield

*Partial albino Great Gray Owl (*Strix nebulosa*) from eastern Idaho.*

This white owl, later determined to be a male, occupied the same breeding area over three seasons and raised three normally plumaged gray owlets in two out of three breeding seasons (Whitfield *et al.* 1995). The female was normally colored. According to Holt *et al.* (1995), two or three partial albino Great Gray Owls have also been seen in Yellowstone National Park by Mr. Terry McEneaney, but further details are lacking on the extent of albinism of these great grays.

In Canada, before mid-1980 Herbert W.R. Copland and Robert W. Nero observed only five Great Gray Owls with some abnormal white feathers during the lengthy process of handling more than 300 live and some 80 dead adult owls (Scriven 1984).

Since mid-1980, there have been two incomplete albino Great Gray Owls reported in Canada. The first white Great Gray Owl was seen in June 1990 near Norway House, Manitoba (Nero 1991). Distinctly different, but a still incomplete albino was sighted in the boreal forests north of Winnipeg in December 1990 (Holland 1991). Thus far, at least six to seven incomplete albino Great Gray Owls have been recorded since 1980 in the United States, Canada, and Finland.

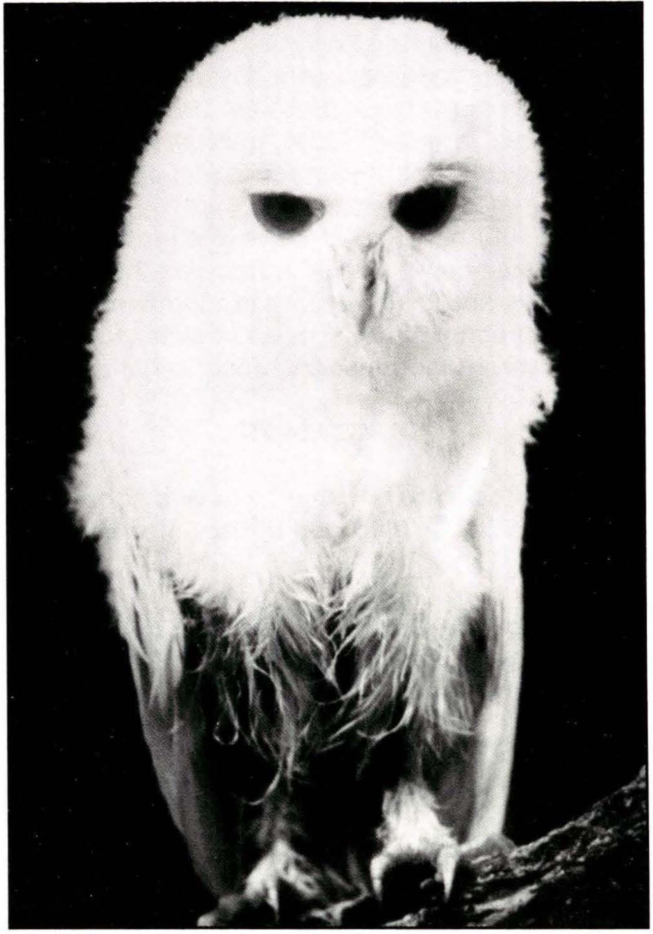
ALBINISM IN OTHER OWLS

Albinism in owls is rare, particularly true albinism (see Gross 1965). Among owls, only the following seven total albinos have been recorded:

1. One total albino Barred Owl (*Strix varia*) was reported from North America by Dean (1976).
2. An albino Eastern Screech-owl (*Otus asio*) reported by Holt *et al.* (1995) from Long Island, New York for at least 5 years from 1982 to 1987.
3. Ross (1973) reviewed albinism in North American birds and also reported a complete albino Eastern Screech-owl specimen, but did not cite the origin of the report.
4. In his book, "A Guide to Birds of Ceylon," G.M. Henry (1969) records that for several years he had a female albino Brown Wood-owl (*Strix leptogrammica*) paired to a normally colored bird. Although she laid eggs, all were infertile.
5. A wildlife rescue organization in Italy received a nestling albino Tawny Owl (*Strix aluco*) which was reared to independence and then released. We have enclosed John Clarke's photograph of it.
6. In Spring 1996, the R.S.P.C.A. Wild Animal Hospital at Somerset, England, also had a young albino Tawny Owl handed in (Bernard C. Sayers 1996).
7. A 'snow white' Short-eared Owl (*Asio flammeus*) was seen on August 19, 1997 in the then "new" Flevopolder near Ketelhaven, the Netherlands (Rudolf F. Koes, pers. comm.).

In addition, we know of the following incomplete albinos:

1. Burrowing Owl (*Speotyto cunicularia*) from the U.S.A. (Sutton 1912).
2. Great Horned Owl (*Bubo virginianus*) from the U.S.A. (Spofford 1952).
3. Short-eared Owl (*Asio flammeus*) from the U.S.A. (Sage 1983).
4. An adult and one young Western Screech-owl (*Otus kennicottii*) observed in Washington State by Terry Flemming (Holt *et al.* 1995).



John Clarke

Total Albino Tawny Owl in Italy.

5. A local population of white Little Owls (*Athene noctua*) in Jerez, Spain; some were exhibited in the Jerez Zoo (Sayers 1996). Although uniformly white, they had normal eye coloring.
6. Antwerp Zoo in Belgium has bred one or more leucistic (isabelline) Spectacled Owls (*Pulsatrix perspicillata*) (Sayers 1996).
7. Bill Ayling, who maintains a small private owl collection in Norfolk, England, bought a pair of Barn Owls (*Tyto alba*) from a breeder in Essex. The male is pure white, although its eyes are of normal coloration (Mikkola and Sayers 1997).
8. B. Sayers has one pair of Indian Scops-owls (*Otus bakkamoena*), which produced a leucistic (isabelline) young in 1994, and again in 1995 and 1996 (Mikkola and Sayers 1997).

9. Lincoln Childrens Zoo in the United States had a pure white Eastern Screech-owl with a few tan feathers on the breast, but the eyes were not pink (Bennett 1969). Earlier this bird was said to be "pure white with pink eyes" (Schneider 1969).

Gross (1965) noted nine cases of albinism from five species of owls in North America, but did not list the species or degree of albinism. It is likely that some of the species of owls cited above were, in fact, also included in his report.

DISCUSSION

Albino animals are thought to have a short life expectancy in the wild due to the following factors:

1. Intraspecific conflict in rejection by their congeners; which particularly applies to gregarious species.
2. Pink-eyed, albinistic birds have poor eyesight, a physical disorder which becomes most acute in bright light.
3. Conspicuous nature of their color makes them more vulnerable to predation. When the mutant is, itself, a predator, an unobserved approach on their prey may be less likely, thereby lowering foraging success.

However, the observations cited in this paper show that albinos and incomplete albinos have paired normally and survived several years in the wild. So owls seem less affected by the above-mentioned problems than most other birds. Abnormal color would only marginally affect a nocturnal predator's hunting success, as most owls locate their prey by sound rather than by sight. Thus, poor eyesight in bright sunlight is not a disability to a nocturnal species (Sayers 1996).

However, it remains a mystery to the authors why so many incomplete albino Great Gray Owls have been recorded since 1980 in the Northern Hemisphere, although albinism in owls is normally extremely rare.

ACKNOWLEDGEMENT

We are most grateful to Mary Maj, Denver Holt, and Bernard C. Sayers who assisted us in collecting all known owl albino cases. Our thanks are also due to Richard J. Clark and John Wilson who agreed to be our peer reviewers.

LITERATURE CITED

Bennett, E.B. 1969. Albino Screech Owl. Nebraska Bird Review. 37: 16.

Dean, R. 1976. Albinism and melanism among North America birds. Bulletin of the Nuttall Ornithological Club. 2: 20-24.

Gross, A.O. 1965. The incidence of albinism in North American birds. Bird-Banding. 36: 67-71.

Henry, G.M. 1969. A guide to the birds of Ceylon. Kandy, Ceylon.

Holland, G. 1991. Second Albino Great Gray Owl sighted in Manitoba. Blue Jay. 49(1): 32.

Holt, D.W.; Robertson, M.W.; Ricks, J.T. 1995. Albino Eastern Screech-owl, *Otus asio*. Canadian Field-Naturalist. 109(1): 121-122.

Lehto, H.J.; Lehto, H. 1995. Leucistic Great Gray Owl in Finland in March-April 1994. Dutch Birding. 1/95: 19-20.

Mikkola, H.; Sayers, B. 1997. Albinism in owls. Tyto. 2(2): in press.

Mueller, C.D.; Hutt, F.B. 1941. Genetics of the fowl, sex-linked imperfect melanism. Journal of Heredity. 32: 71-80.

Nero, R.W. 1981. White Great Gray Owl. Blue Jay. 49(1): 31.

Ross, C.C. 1973. Some additional records of albinism in North American birds. Cassinia. 54: 18-19.

Sage, J.H. 1983. A partial albino Short-eared Owl. Bulletin of the Nuttall Ornithological Club. 8: 183.

Sayers, B. 1996. A personal view of colour mutations. Tyto. 1(1): 24-29.

Schneider, J. 1969. Albino Screech Owl. Nebraska Bird Review. 37: 16.

Scriven, R. 1984. A note on albinism in the Great Gray Owl. Blue Jay. 42(3): 173-174.

Spofford, W.R. 1952. A partial albino Horned Owl. Kingbird. 2: 84.

Sutton, G.M. 1912. An Albinistic Burrowing Owl. Bird Lore. 14: 184.

Wanders, I. 1994. Albino Great Gray Owl in Finland. Blue Jay. 52(4): 228.

Whitfield, M.B.; Maj, M.E.; Kelley, J. 1995. Incomplete albino Great Gray Owl in Idaho. Blue Jay. 53(4): 197-199.

Breeding Biology of the Barn Owl (*Tyto alba*) in the Lower Mainland of British Columbia

Lorraine A. Andrusiak and K.M. Cheng[1]

Abstract.—Breeding of the Barn Owl was studied from 1990-1992 in the Lower Mainland of British Columbia, the northern limit of the species' North American range. Over 3 years, mean clutch size was 6.5 ± 3.5, mean brood size at time of banding was 3.3 ± 2.0, and mean number of nestlings fledged was 2.6 ± 2.1. Clutch size ranged from 2 to 18 eggs. There were no significant differences in fledging success rates between years. Severe weather in 1991 resulted in high Barn Owl mortality. If the number of nestlings banded per year is used as an index of productivity and the number of barn owl carcasses reported per year is used as an index of mortality, the year of 1991 has both the highest mortality and the lowest productivity of the 3 years. The use of man-made sites by Barn Owls for roosting and nesting provides increased thermal cover and security from predators which may be vital for the species at the northern limit of its distribution.

The Barn Owl (*Tyto alba pratincola*) is classified as "uncommon to very rare" throughout British Columbia (Campbell *et al.* 1990). The species was first recorded in the province in 1909 and there were no breeding records until 1941 (Cowan 1942), making the Barn Owl a relatively recent addition to the province's fauna. The Barn Owl favors open habitat and is often closely associated with agricultural areas (Bent 1961, Campbell and Campbell 1983, Marti 1992a). The Barn Owl's primary prey species in the Lower Mainland is the Townsend's vole (*Microtus townsendii*), which inhabits old fields and other grassland habitats throughout the Lower Mainland (Campbell 1983). It is probable that the clearing of forested lands and the development of agriculture in the Lower Mainland provided the open habitat necessary for the Barn Owl to expand its range northward into British Columbia. Today the British Columbia population of Barn Owls is estimated to be about 1,000, with the species breeding from southern Vancouver Island through the Lower Mainland as far east as Hope (Campbell and Campbell 1983). The Barn Owl is a blue-listed species (vulnerable or sensitive species) in the provincial wildlife listing system. Current breeding records of Barn Owls elsewhere in Canada are extremely rare. The Lower Mainland population represents the northernmost edge of the Barn Owl's North American breeding range (fig. 1).

Barn Owl populations are declining in many parts of the world due to changes in agricultural practices and climate (Bunn *et al.* 1982, Shawyer 1987, Marti 1992a). Barn Owls are intolerant of cold winters in general and long-lasting snow in particular (Stewart 1952, Henny 1969, Glue and Nuttall 1971, Marti and Wagner 1985, Madge and Tyson 1987, Shawyer 1987, Taylor 1989), and the species breeds successfully only in temperate climates. Barn Owls have narrow thermoneutral zones, relatively poorly-insulating plumage and scant fat reserves (Johnson 1974). Deep snow provides a physical barrier between the Barn Owl and its small mammal prey and appears to greatly diminish hunting success. Research on the Barn Owl in British Columbia has been confined mainly to food-habits studies (Cowan 1942, Dawe *et al.* 1978, Campbell 1983, Campbell *et al.* 1987). Without data on the owl's reproductive and mortality patterns within the Lower Mainland it is difficult to devise management options to conserve the species. The objectives of this study were to

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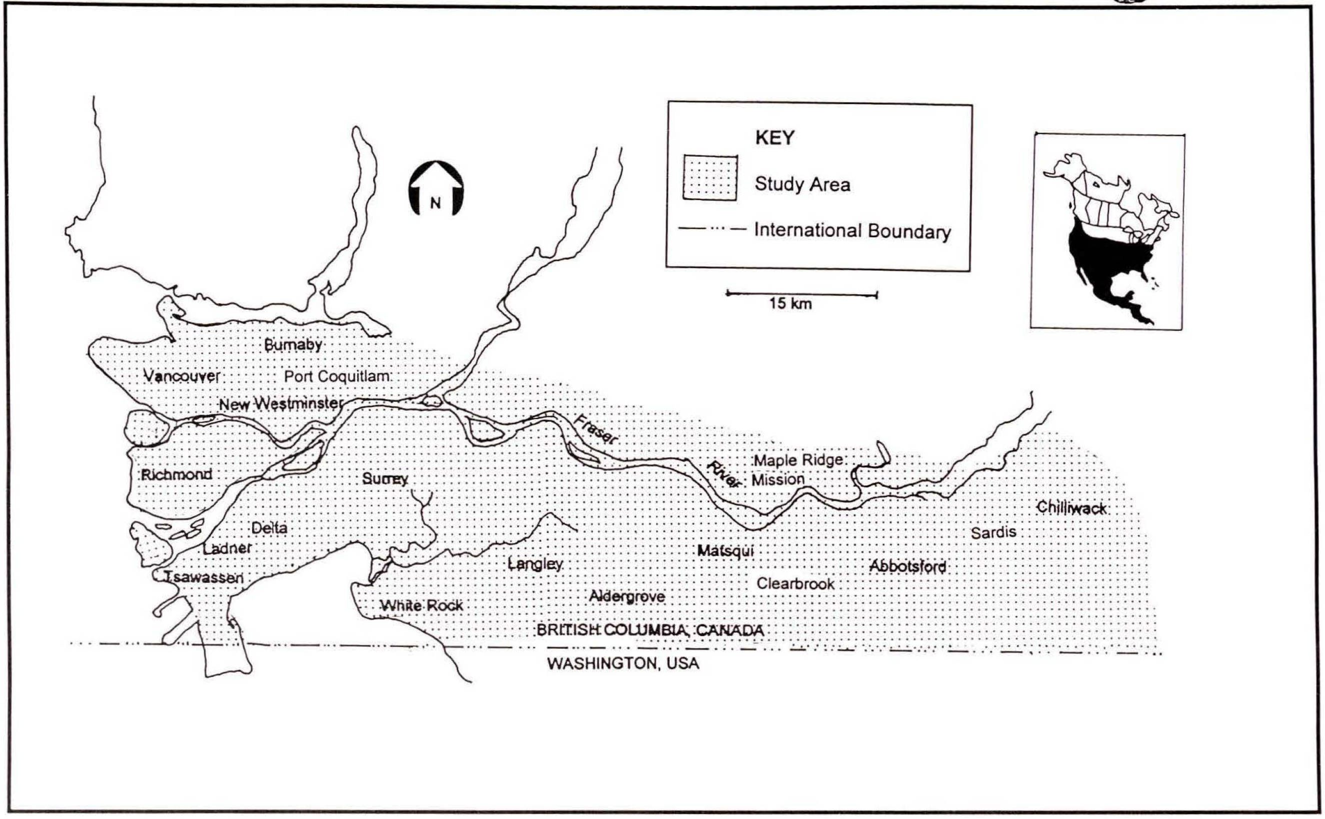
KEY
Study Area
International Boundary
15 km
N
Burnaby
Vancouver
Port Coquitlam
New Westminster
Fraser
River
Maple Ridge
Mission
Richmond
Surrey
Delta
Ladner
Tsawassen
Chilliwack
Sardis
Matsqui
Abbotsford
Clearbrook
Langley
Aldergrove
White Rock
BRITISH COLUMBIA, CANADA
WASHINGTON, USA

Figure 1.—*The study area in British Columbia's Lower Mainland. Inset: the Barn Owl's North American breeding range (redrawn from Marti 1992a).*

gather baseline data on reproductive success and mortality and to correlate it with environmental conditions.

STUDY SITE

The Lower Mainland region of British Columbia constitutes approximately 300,000 ha in the extreme southwest corner of the province (fig. 1). This area includes the districts and municipalities of Vancouver, Burnaby, Richmond, Delta, Tsawwassen, Surrey, Langley, Aldergrove, Matsqui, Abbotsford, Clearbrook, Port Coquitlam, Pitt Meadows, Mission, Maple Ridge, Sardis and Chilliwack. The Lower Mainland is bordered by the North Shore Mountains to the north, and by the United States to the south. Westward, the area is bounded by the Strait of Georgia, while to the east the mountains of the Coastal and Cascade ranges form a natural barrier. The Fraser River travels a sinuous course through the middle of the Fraser Valley and is a major influence on topography and vegetation. Very little of the original virgin coniferous forest now remains in the Lower Mainland, but extensive areas of second-growth forest exist in the adjacent uplands. The study site lies in the Coastal Western Hemlock (CWH) biogeoclimatic zone (Meidinger and Pojar 1991). The main subzones are the CWH dry maritime (CWHdm) and the CWH very dry maritime (CWHxm). The climate of the region is moderate, with cool summers and mild, wet winters (Stager and Wallis 1968). The mean annual temperature is approximately 10°C, with January temperatures usually above freezing. The number of frost-free days per year is usually well above 200. Between 750 to 1,016 mm of precipitation falls per year, with 30-40 percent occurring during December, January, and February. Only 4-6 percent of the precipitation occurs as snow (Stager and Wallis 1968). The Lower Mainland has the mildest climate in Canada (Hunter 1996).

Approximately 2 million people reside in the Lower Mainland (Hunter 1996). Urban areas cover approximately 91,000 ha, and land classified as undisturbed (mainly second-growth forest) makes up a further 72,000 ha. Most of the remainder is agricultural land (Moore 1990), including mixed farms, large dairy farms, small hobby farms, and berry farms.

METHODS

Sites used by Barn Owls were located by a variety of methods. Drive-by surveys began in January of 1990 and were conducted in rural areas to locate structures that might be used by owls. Posters explaining the project were distributed to farm supply, feed and pet stores, and were posted at agricultural exhibitions and shows. Two local wildlife shelters provided addresses of persons bringing in orphaned or moribund Barn Owls. Television and newspaper reports publicizing the project identified potential nest sites, and the local Ministry of the Environment office (Region II) referred others to us.

Non-breeding Barn Owls frequently roost at the same locations where they breed. Sites where nesting had occurred or could potentially occur were monitored. Nest inspections were done periodically from January 1990 to May 1993. Level of effort to visit nests was reduced during the fall of 1990. Other than this, similar levels of effort were made in all 3 years to visit nests, but due to access problems with property owners it was not possible to visit the same sample of sites every year. Attempts were made to visit each site monthly during the prime breeding season (March to November) to determine if nesting had been initiated and at least once during the rest of the year. Barn Owls frequently desert nests if disturbed during incubation. If nest inspections flushed an incubating owl, the clutch was counted and observers then left the area as quickly as possible. If observation at a distance revealed an incubating owl, the bird was not flushed and no data on clutch size was recorded.

Nestling owls were large enough to band after the age of about 3 weeks. The normal procedure was to climb to the nest, one by one place each nestling into a deep plastic pail and lower the pail by means of a rope to an assistant. Standard measurements (wing chord, tarsus length, tarsus width, talon length, and beak length) were taken, and weight was determined with a spring scale. The number of nestlings in the brood at the time of banding (brood size) was recorded. All nestlings were banded with Canadian Wildlife Service standard numbered aluminum leg bands. Each nestling was then hauled back up in the pail and replaced at the nest. Handling and banding of nestlings was assumed to have no effect on fledging success (Taylor 1991). Each banding site was revisited after the young had fledged. Accumulated pellet material in the nest site was sifted to find any remains (bands and bones) of nestlings which failed to fledge. The area for 50 m around the nest site was also searched for nestling remains. If no remains were found, all nestlings were assumed to have fledged successfully.

Information on mortality patterns of wild, fledged Barn Owls was obtained from British Columbia Ministry of the Environment (Region II) taxidermy permit records. Members of the public finding dead owls brought them to the Ministry office for taxidermy permits. Staff biologists examined, weighed and measured each carcass, and assigned a probable cause of death based on the condition of the carcass (i.e., broken bones, emaciation) and recorded other information from the finder. Information on local weather patterns was obtained from published Environment Canada records from the meteorological station at the Vancouver International Airport.

RESULTS

Two hundred thirty-six sites used by Barn Owls for roosting and/or nesting were located in the Lower Mainland. All but nine of these were man-made sites. Barns made up the greatest proportion of Barn Owl sites, comprising 72 percent of the total. Nesting attempts were recorded at 48 different sites during the 3-year study. A total of 119 Barn Owl carcass records from 1990-1992 were tabulated. Further examination of Barn Owl mortality data will be presented in another paper (Andrusiak and Cheng, Canadian Field-Naturalist, pending).

Two successful nests per year at the same site were recorded once during each of 1990 and 1991. Three instances of two successful nests at the same site within the same year, and three replacement nests (of unsuccessful breeding attempts) were recorded in 1992.

A summary of Barn Owl reproduction over the 3 years is presented in tables 1 and 2. There were no significant differences in clutch size over the 3 years, probably due to the small sample size. Clutch sizes varied from 2 to 18, with 5 eggs being the most common. Included in the data are observations of two unusually large clutches (14 and 18 eggs), both of which failed to hatch, recorded in consecutive years

Table 1.—*Barn Owl reproductive success in the Lower Mainland of British Columbia, 1990-1992—all nests.*

Year	Mean Clutch	N	Mean Brood	N	Mean # Fledged	N
1990	7.4 ±4.0	5	3.2 ±2.3	18	2.9 ±2.2	18
1991	4.0 ±1.6	3	2.2 ±1.3	17	2.1 ±1.2	15
1992	6.7± 3.4	15	3.8 ±2.0	35	2.7 ±2.3	29
Total	6.5 ±3.5	23	3.3 ±2.0	70	2.6 ±2.1	62

Table 2.—*Barn Owl reproductive success in the Lower Mainland of British Columbia—successful nests only (at least 1 young fledged).*

Year	Mean Clutch	N	Mean Brood	N	Mean # Fledged	N
1990	8	1	4.1 ±1.7	14	4.1 ±1.9	14
1991	4	1	2.5 ±1.2	11	2.4 ±0.9	13
1992	6.0 ±1.8	9	4.1 ±1.9	20	3.8 ±1.9	21
Total	5.8 ±1.8	11	3.7 ±1.8	45	3.4 ±1.8	48

at the same nest site. It is possible that these were produced by the same pair and that both members of the pair were females, although same-sex pairs have not been documented for this species.

The number of juveniles observed at banding (brood size) from nests where incubation was known to occur ranged from 0 to 8 (fig. 2). Mean brood size and the mean number of young fledged per nest were not significantly different over the 3 years (tables 1 and 2). Unusually large and long-lasting snowfalls were notable for 1991. There was an inverse relationship between the total number of nestlings banded per year and the number of days with snow cover the previous winter (fig. 3). Less variation in brood size (number of nestlings per nest) was noted during 1991 (fig. 2).

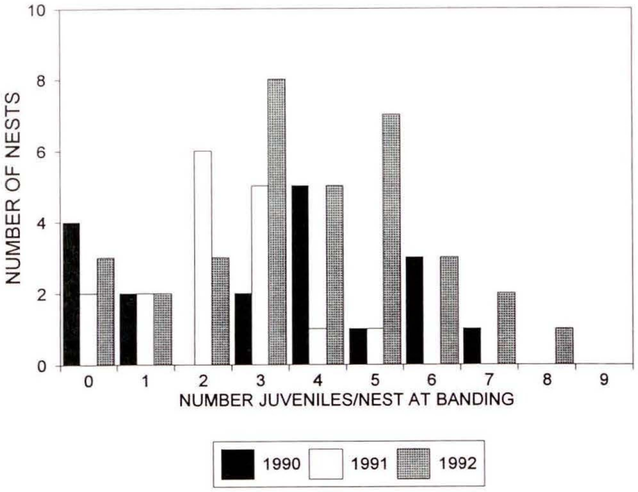

Figure 2.—*Barn Owl brood sizes in the Lower Mainland of British Columbia 1990-1992 (N=70).*

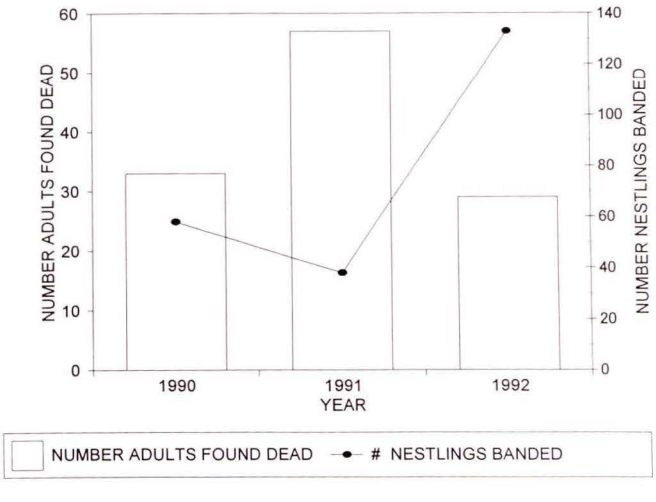

Figure 3.—*Number of days of lying snow (snowdays) per winter in the Lower Mainland of British Columbia and number of Barn Owl nestlings banded the following summer.*

The seasonal pattern of reproduction was bimodal, with the largest peak in numbers of nestlings banded occurring in late spring to early summer, and a second, smaller peak occurring during the fall (fig. 4). In 1991, peak numbers of nestlings were banded 1 month later than in 1990 or 1992, demonstrating that egg-laying was delayed that year.

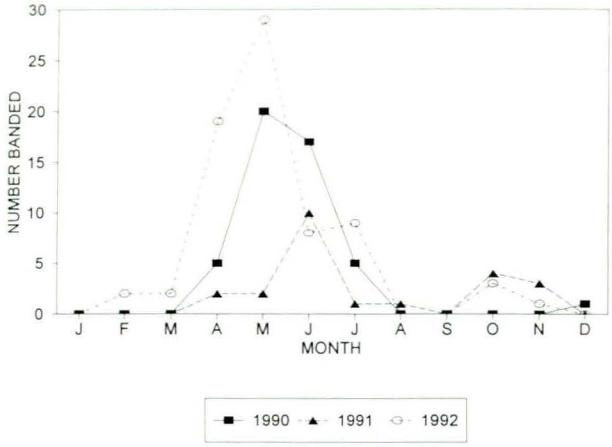

Figure 4.—*Number of nestling Barn Owls banded by month, 1990-1992 in the Lower Mainland of British Columbia.*

If the total number of nestlings recorded/year is used as an index of productivity and the number of carcasses turned into the Ministry of the Environment is used as an index of mortality (fig. 5), 1991 had both the highest mortality ($\chi^2 = 11.58$, $p < 0.05$, df = 2; Bonferroni z test) and the lowest productivity of the 3 years ($\chi^2 = 38.01$, $p < 0.05$, df = 2; Bonferroni z test). The greatest proportion of successful nests also occurred in 1991 (table 3). Seventy-seven percent of the observed nests over the 3 years successfully fledged young, and the overall percentage of nestlings fledged was 80 percent. In Mali, most Barn Owl pre-fledging mortality occurred before Day 15 (Wilson *et al.* 1985). If this is also the case in the Lower Mainland, most nestling mortality would have occurred before the nestlings were banded (counted), resulting in the small observed difference between the mean brood size and mean number fledged.

DISCUSSION

Productivity declined and mortality increased during 1991, a year noted for its snowy, cold winter. These results were probably due to a combination of fewer owls surviving the winter to breed and poor foraging weather during the nestling season. Yet, the same year (1991) also had the greatest proportion of successful nests. This apparent contradiction may be due to young owls making up the largest proportion of winter deaths and therefore relatively fewer young owls nesting the following spring. It is likely that impaired hunting success due to persistent snow cover would be most serious for younger birds with less hunting experience. If older birds are initiating the majority of the nesting attempts, their parental and hunting experience may account for the larger proportion of successful nests. It is also possible that young owls may delay the onset of reproduction under poor conditions. Female Ural Owls (*Strix uralensis*) have been observed to postpone their first breeding attempt when faced with poor environmental conditions (Pietiainen 1988).

Other studies have found similar variations in Barn Owl reproduction with environmental

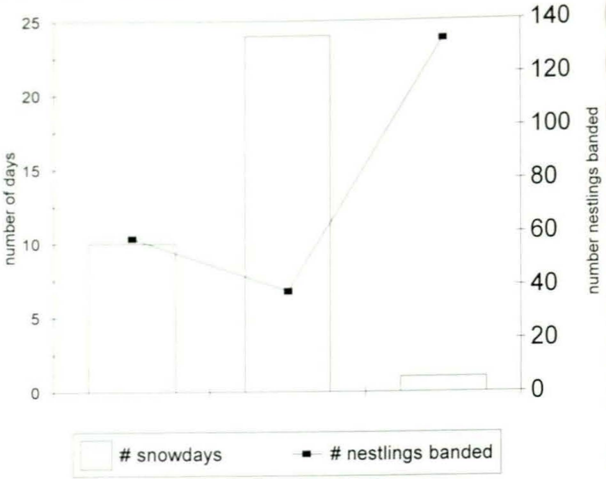

Figure 5. —*Barn Owl production and mortality, 1990-1992 in the Lower Mainland of British Columbia.*

Table 3.—*Percentage of successful Barn Owl nests and nestlings fledged in the Lower Mainland of British Columbia.*

Year	N	Successful nests	Nestlings fledged
		- - - - - - *Percent* - - - - - -	
1990	18	78	93
1991	15	86	89
1992	29	72	71
Total	70	77	80

conditions. The number of nesting attempts, mean clutch size, and mean number of young fledging from successful nests all declined the year following a severe winter in Utah (Marti and Wagner 1985). Marti (1992b) also found that persistent snow cover and low winter temperatures significantly delayed the onset of egg laying and reduced the number and success of breeding attempts during a 16-year study of Barn Owl reproduction in Utah. Braaksma and de Bruijn (1976) reported Barn Owl population fluctuations with climate in Holland, and Henny (1969) found that annual rates of Barn Owl production varied.

The increase in double broods and replacement broods noted in 1992 demonstrates that the population has the potential for rapid expansion after a poor year. The Barn Owl's relatively large clutch size and its ability to raise more than one brood per year under good conditions allow populations to swiftly recover. This reproductive potential is consistent with an r-selected life history strategy (Colvin *et al.* 1984).

In the Lower Mainland Barn Owls appear to depend heavily on farm buildings, especially barns, for use as roosting and nesting habitat. Considerable research has been done on the microclimates of roost and nest sites and the effects of nest insulation (Calder 1973; Bartholomew *et al.* 1976; Francis 1976; Mayer *et al.* 1982; Walsberg 1985, 1986; Millsap and Millsap 1987), and some studies have found relationships between microclimate and birds' energy budgets and/or reproductive success (Kendeigh 1961, White *et al.* 1975, Austin 1976, Kelty and Lustick 1977). Other researchers (Johnson 1974, Campbell and Campbell 1983) have suggested that the use of man-made structures is particularly important to Barn Owls inhabiting the northern limits of their range. A sheltered place to roost may enable an owl to conserve energy otherwise lost to thermogenesis, thus increasing survival when temperatures are low and small mammals are scarce or unobtainable due to snow cover (Hayes and Gessaman 1980).

Although sample sizes are limited, some general observations can be made from the nest and reproduction data. Excluding the two abnormally large (and unsuccessful) clutches, clutch sizes were consistent with that reported elsewhere (table 4). Brood size and number of fledged young per nest, although consistent with that from other studies, were somewhat lower (table 4). Given the similarities to other studies in regards to the type of nest site (barns), foraging habitat (grass fields), and prey base (*Microtus* ssp.), but more challenging weather conditions (colder temperatures), our results are consistent with that which might be expected for an animal on the edge of its range. Of note is the apparent magnitude of the population change between years. Further study may offer insights as to the causal mechanism behind the annual fluctuations. Investigations on the Townsend's Vole have indicated that while numbers of this important prey vary yearly from field to field, it does not appear to cycle uniformly across the lower mainland of British Columbia (Mary Taitt pers. comm.).

Table 4.—*Comparison of Barn Owl reproductive data from various sources.*

Source	**Area**	**Clutch size**	**N**	**# Fledged/nest**	**N**
This study	British Columbia	6.5 ± 3.5[1]	23[1]	2.6 ± 2.1	62
Ault 1982	Oklahoma	-	-	2.8 ± 0.3	55
Millsap and Millsap 1987	Colorado	4.6 ± 0.4	14	2.3 ± 0.6	14
		5.3 ± 0.8	10	3.9 ± 0 .8	10
Otteni *et al.* 1972	southern Texas	4.9 ± 1.4	91	2.0 - 3.2	71
Marti 1992b	Utah	7.2	275	5.1	275
Shawyer 1987	Great Britain	4.9	125	3.0	290
Wilson *et al.* 1985	central Mali	6.1 ± 1.5	140	1.8 ± 2.5	136

[1] Clutch size calculations includes two unsuccessful nests containing 14 and 18 eggs. Excluding these from the sample gives a mean clutch size of 5.6 eggs/clutch.

Management strategies intended to maintain Barn Owl populations in the province will need to recognize the species' vulnerability to severe winter weather. Although recovery following a bad year can be swift, a succession of poor years might decimate the small Lower Mainland population. The population would, however, probably be supplemented by immigration from the south and recover its present level over several years.

CONCLUSIONS

Productivity and mortality of Barn Owls in the Lower Mainland appears to be correlated with the persistence of snow cover during the winter. Increased duration of snow cover results in higher levels of adult winter mortality as well as decreased productivity during the following breeding season. Barn Owls in the Lower Mainland appear to depend heavily on man-made structures for roosting and nesting, perhaps due to the shelter they provide. The Barn Owl's vulnerability to severe winter weather has important implications for conservation of this species in Canada.

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LITERATURE CITED

Andrusiak, L.; Cheng, K. 1997. Mortality and dispersal of the Barn Owl (*Tyto alba pratincola*) in the Lower Mainland of British Columbia. Canadian Field Naturalist. (submitted).

Ault, J.W. 1982. A quantitative estimate of barn-owl nesting habitat quality. Stillwater, OK: Oklahoma State University. M.S. thesis.

Austin, G.T. 1976. Behavioral adaptations of the Verdin to the desert. Auk. 93: 245-262.

Bartholomew, G.A.; White, F.N.; Howell, T.R. 1976. The thermal significance of the nest of the Sociable Weaver, *Philetairus socius*: Summer observations. Ibis. 118: 402-410.

Bent, A.C. 1961. Barn Owls. In: Life histories of North American birds of prey (Part 2). Bull. 170. New York, NY: U.S. National Museum.

Braaksma, S.; De Bruijn, O. 1976. De kerkuilstand in Nederland. Limosa. 49: 135-187.

Bunn, D.S.; Warburton, A.B.; Wilson, R.E.S. 1982. The Barn-owl. Staffordshire: T. & A. D. Poyser.

Calder, W.A. 1973. Microhabitat selection during nesting of hummingbirds in the Rocky Mountains. Ecology. 54: 127-134.

Campbell, E.C.; Campbell, R.W. 1983. Status report on the Common Barn-Owl (*Tyto alba*) in Canada - 1982. Victoria, BC: Committee on the Status of Endangered Wildlife in Canada, British Columbia Ministry of the Environment.

Campbell, R.W. 1983. Feeding ecology of the Common Barn Owl in North America. Seattle, WA: University of Washington. M.S. thesis.

Campbell, R.W.; Manuwal, David A.; Harestad, Alton S. 1987. Food habits of the Common Barn-owl in British Columbia. Canadian Journal of Zoology. 65: 578-586.

Campbell, R.W.; Dawe, N.K.; McTaggart-Cowan, I.; Cooper, J.M.; Kaiser, G.W.; McNall M.C.E. 1990. The birds of British Columbia. Vol. 2, Non-passerines. Diurnal birds of prey through woodpeckers. Victoria: Royal British Columbia Museum.

Colvin, B.A.; Hegdal, P.L.; Jackson, W.B. 1984. A comprehensive approach to research and management of Common Barn Owl populations. In: Proceedings of Workshop on management of nongame species and ecological communities; 1984 June 11-12; University of Kentucky.

Cowan, I. McT. 1942. Food habits of the Barn-owl in British Columbia. Murrelet. 2: 349-53.

Dawe, N.K.; Runyan, C.S.; McKelvey, R. 1978. Seasonal food habits of the Barn-owl (*Tyto alba*) on the Alaksen National Wildlife Area, British Columbia. Canadian Field Naturalist. 92: 151-155.

Francis, W.J. 1976. Micrometeorology of a blackbird roost. Journal of Wildlife Management. 40: 132-136.

Glue, D.E.; Nuttall, J. 1971. Adverse climactic conditions affecting the diet of a Barn-owl in Lancashire. Bird Study. 18(1): 33-34.

Hayes, S.R.; Gessaman, James A. 1980. The combined effects of air temperature, wind and radiation on the resting metabolism of avian raptors. Journal of Thermal Biology. 5: 119-125.

Henny, C.J. 1969. Geographical variation in mortality rates and production requirements of the Barn Owl (*Tyto alba ssp.*) Bird-banding. 40: 277-356.

Hunter, L., ed. 1996. Vancouver and British Columbia. Moving To and Around. 23 (5): 23-39.

Johnson, W.D. 1974. Bioenergetics of the Barn Owl (*Tyto alba*). Long Beach, CA: California State University. M.S. thesis.

Kelty, M.P.; Lustick, S.I. 1977. Energetics of the Starling (*Sturnus vulgaris*) in a pine woods. Ecology. 58: 1181-1185.

Kendeigh, S. Charles. 1961. Energy of birds conserved by resting in cavities. Wilson Bulletin. 73: 140-147.

Madge, G.; Tyson, K. 1987. Decline of the Barn Owl in relation to mid-Devon weather records. Devon Birds. 40: 84-87.

Marti, Carl D. 1992a. Barn Owl (*Tyto alba*). In: Poole, A.; Stettenheim, P.; Gill, F., eds. The birds of North America, No. 1. Philadelphia, PA: The Academy of Natural Sciences; Washington, DC: The American Ornithologists' Union.

Marti, Carl D. 1992b. Barn Owl reproduction and its constraints near the limit of the species' distribution. In: Proceedings of the Raptor Research Foundation Inc. Annual meeting; 1992 November 11-15; Bellevue, WA: Raptor Research Foundation.

Marti, C.D.; Wagner, P.W. 1985. Winter mortality in Common Barn-owls and its effect on population density and reproduction. Condor. 87: 111-115.

Mayer, L.; Lustick, S.; Battersby, B. 1982. The importance of cavity roosting and hypothermia to the energy balance of the winter acclimatized Carolina Chickadee. International Biometeorology. 26: 231-238.

Meidinger, D.; Pojar, J. 1991. Ecosystems of British Columbia. Victoria, BC: Research Branch, B.C. Ministry of Forests.

Millsap, B.A.; Millsap, P.A. 1987. Burrow nesting by Common Barn-owls in north central Colorado. Condor. 89: 668-670.

Moore, K. 1990. Urbanization in the Lower Fraser Valley, 1980-1987. Tech. Rep. Ser. 120. Ottawa: Canadian Wildlife Service.

Otteni, Lee C.; Bolen, Eric G.; Cottam, Clarence. 1972. Predator-prey relationships and reproduction of the Barn Owl in southern Texas. Wilson Bulletin. 84: 434-448.

Pietiainen, H. 1988. Breeding season, quality, age, and the effect of experience on the reproductive success of the Ural Owl (*Strix uralensis*). Auk. 105: 316-324.

Shawyer, C. 1987. The Barn-owl in the British Isles - its past, present and future. London: The Hawk Trust.

Stager, J.K.; Wallis, J.H. 1968. The climatic factor - variations on a mean. In: Siemens, A.H., ed. Lower Fraser Valley - evolution of a cultural landscape. B.C. Geograph. Ser. 9. Victoria, BC: Tantalus Research Limited: 89-100.

Stewart, Paul A. 1952. Winter mortality of Barn Owls in central Ohio. Wilson Bulletin. 64: 164-166.

Taylor, I.R. 1989. The Barn-owl. Shire Nat. His. Ser. 4. Aylesbury, Bucks, England: Shire Publications Ltd: 21-24.

Taylor, I.R. 1991. Effects of nest inspections and radio-tagging on Barn Owl breeding success. Journal of Wildlife Management. 55(2): 312-315.

Walsberg, G.E. 1985. Physiological consequences of microhabitat selection. In: Habitat selection in birds. New York, NY: Academic Press: 389-413.

Walsberg, G.E. 1986. Thermal consequences of roost-site selection: the relative importance of three modes of heat conservation. Auk. 103: 1-7.

White, F.N.; Bartholomew, G.A.; Howell, T.R. 1975. The thermal significance of the nest of the Sociable Weaver *Philetairus socius*: Winter observations. Ibis. 117: 171-179.

Wilson, R.T.; Wilson M.P.; Durkin, J.W. 1985. Breeding biology of the Barn Owl *Tyto alba* in central Mali. Ibis. 128: 81-90.

Dispersal Movements of Juvenile Mexican Spotted Owls (*Strix occidentalis lucida*) in New Mexico

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Abstract.—Tail-mounted radio transmitters were attached to 12 juvenile and 3 sub-adult (yearling) Mexican Spotted Owls (*Strix occidentalis lucida*) in southwestern New Mexico from 1993 to 1996. Most juveniles dispersed from their natal territories during September. Intervals between dispersal of siblings ranged from 3 to more than 15 days. Juveniles exhibited two types of dispersing behavior; moving rapidly across the landscape (up to 11.3 km/night) and extensive local exploration. Two juveniles moved between separate mountain ranges and crossed at least 25 km of grassland and pinon/juniper (*Pinus/Juniperus* spp.) savanna habitat, suggesting that isolated populations in the southwest U.S. could function as a metapopulation. During dispersal juveniles were found to roost in habitat unlike that normally used by adults, including open ponderosa pine (*Pinus ponderosa*) and pinon/juniper habitat. The three sub-adult females paired temporarily with adult males in their first summer, but then left in the fall, suggesting that dispersal can continue through an owl's second year.

Dispersal is the movement an individual makes from its birth site to first breeding site (natal dispersal) or movement between successive breeding sites (breeding dispersal; Greenwood 1980). Dispersal can play an important role in population dynamics, and is known to have a large influence on the genetic structure of populations (Brookes and Butlin 1994, Slatkin 1985, Stacey and Taper 1992, Verhulst *et al.* unpubl. data, Wright 1951, Zink and Dittman 1993). Therefore, characterizing dispersal behavior is critical to understanding the demography and population structure of species, especially the persistence of rare and endangered species.

The Mexican Spotted Owl (*Strix occidentalis lucida*) is found in forested mountain and deep canyon terrain throughout the southwest U.S. and into Mexico (Ganey and Balda 1989). In southwestern New Mexico, spotted owls roost in riparian/canyon bottom or mixed conifer/oak habitats (Hodgson and Stacey 1997). Nests are located in caves or large trees with high canopy closure, most often Douglas-fir (*Pseudotsuga menziesii*; see also Seamans and Gutierrez 1995). Adult spotted owls have high breeding site fidelity with only a few cases of breeding dispersal observed (Gutierrez *et al.* 1996). Therefore, the majority of individuals that disperse are juveniles.

There is evidence that the Mexican Spotted Owl's distribution was once more continuous, occupying lowland riparian forests dominated by cottonwoods (*Populus* spp.) (Bendire 1892, Phillips *et al.* 1964, Woodhouse 1853). Spotted owl habitat is presently fragmented in New Mexico, and owls are restricted to the higher elevations of isolated mountain ranges (fig. 1). Furthermore, annual variation in reproductive success is high, with few or no young produced in some years (Miller 1989, Forsman *et al.* 1984, this study). Demographic models predict that small, isolated populations with high variance in reproductive success should quickly go extinct, unless the populations are connected to other populations by dispersal, thus forming a larger metapopulation (Gilpin

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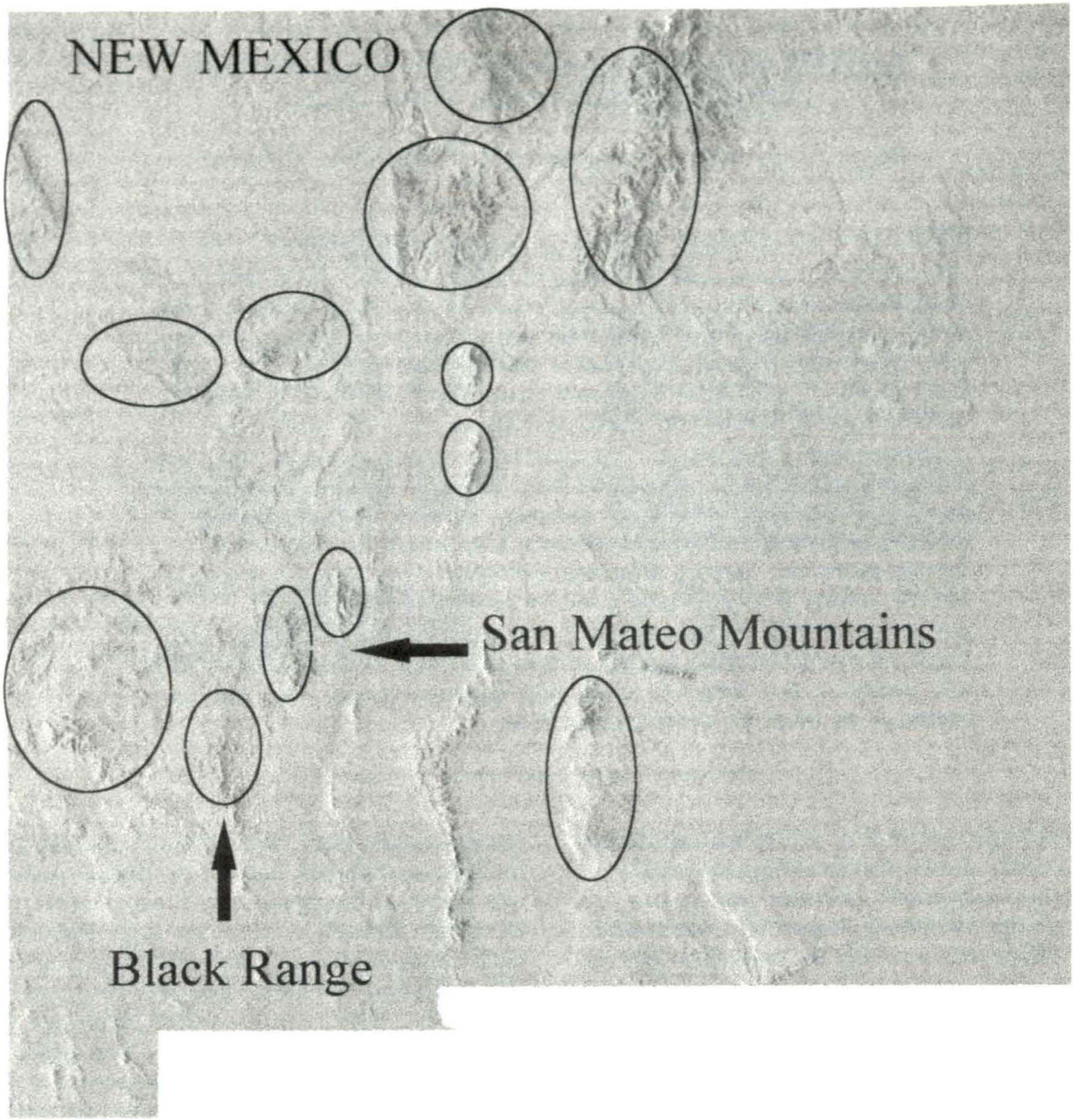

Figure 1.—*The fragmented distribution of the Mexican Spotted Owl in New Mexico, occurring within the circled mountain ranges, and the location of the Black Range and San Mateo Mountains. Map scale is 1:3,520,000.*

and Hanski 1991, Levins 1969, Stacey and Taper 1992, Stacey *et al.* 1997). If Spotted Owl populations in isolated mountain ranges are connected, owls must disperse across large areas of unsuitable habitat, including grassland and pinon/juniper (*Pinus/Juniperus* spp.) savanna habitat, to reach other populations. Here we consider initial dispersal movements of juvenile Mexican Spotted Owls away from their natal areas.

STUDY AREA

We studied dispersal of the Mexican Spotted Owl in the Black Range and San Mateo Mountains of southwestern New Mexico (fig. 1). The Black Range runs 90 km north-south and is located in the Gila National Forest, 60 km west of Truth or Consequences, New Mexico. The San Mateo Mountains run 55 km north-south and are located in the Cibola National

Forest, 50 km southwest of Socorro, New Mexico. These mountain ranges contain few roads and include three National Forest Service Wilderness Areas. They are separated from each other by approximately 20-40 km of grassland and pinon/juniper savanna habitat characterized by widely scattered low trees in a grass matrix (Dick-Peddie 1993). The topography within the mountain ranges is dominated by high mesas, mountain peaks and deep forested canyons. Spruce-fir forest is found on the high mountain peaks, usually above 2,800 m. Mixed conifer forests consisting of Douglas-fir, white fir (*Abeis concolor*), ponderosa pine, southwestern white pine (*Pinus strobiformis*), aspen (*Populus tremuloides*) and often a component of gambel oak (*Quercus gambelii*) are usually found on north and east facing slopes at middle elevations of about 2,400-3,100 m. Gambel oak and remnant narrowleaf cottonwood (*Populus angustifolia*) are found in most canyon bottoms. Warm and dry woodlands consisting primarily of ponderosa pine, Colorado pinyon (*Pinus edulis*), alligator juniper (*Juniperus deppeana*), one-seed juniper (*Juniperus monosperma*), and gray oak (*Q. Grisea*) are found at elevations generally below 2,600 m, on south and west-facing mountain slopes, and on ridge-tops and mesas (Dick-Peddie 1993).

METHODS

Nocturnal calling techniques (Forsman 1983) were used to detect Mexican Spotted Owls from 1993 to 1996. Surveys were done from April through August by walking along canyon bottoms, with potentially suitable habitat, and regularly imitating a spotted owl four-note location call. Roost trees and nests were located during the day by searching areas where owls were detected during surveys. Owl pairs were determined to be nesting by repeated observations, particularly listening for female contact whistles and juvenile vocalizations from nests at dawn and dusk. Owls were captured with a Bal-chatri trap baited with mice or a 3.4 m noose pole (Forsman 1983). Each captured owl was fitted with a combination of a USFWS aluminum band on one leg and a plastic color band on the other. Wing chord, retrix length, and weight were taken, plumage characteristics noted and about 200 ul of blood taken from the brachial artery. Owls were sexed by behavior, vocalizations, and weight. Juveniles cannot be sexed with these criteria. Age was determined to be juvenile, sub-adult or adult by plumage characteristics (Forsman 1981). A sub-adult can be identified by white tipped retrices which are maintained until approximately 26 months old.

Tail-mounted radio transmitters (5 g or 7.5 g; Holohil Systems, Ltd., Woodlawn, Ontario, Canada) with a battery life of approximately 12 to 18 months were used. These were attached to the underside of the center retrices of juveniles no sooner than 50 days post-fledging when their retrices reached at least 185 cm in length. A TRX 1000S radio-telemetry receiver and a three element Yagi antennae (Wildlife Materials, Inc, Carbondale, IL) were used to track juveniles from the ground. Prior to dispersal, juveniles were located one to seven times per week at their roost sites as well as periodically at night while foraging, depending on the accessibility of their locations. Home range sizes of juveniles prior to dispersal were determined using the minimum convex polygon method with Calhome, a home range analysis program (U.S. Forest Service, Pacific Southwest Research Station, Fresno, CA). Juveniles were located as frequently as possible once dispersal began, facilitated by two telemetry flights in 1993, one in 1994, and four in 1996 (kindly provided by U.S. Fish and Wildlife Service in 1996). Aerial surveys consisted of flying transects throughout the study area while scanning for frequencies either manually or with a ATS R2100 automatic scanning receiver (Advanced Telemetry Systems, Inc., Isanti, MN) from an aircraft equipped with two wing antennas and an antennae switching box.

RESULTS

Observations of juvenile dispersal behavior reported here were from five juveniles from three nests in 1993 and seven juveniles from four nests in 1996. Reproduction in the study area was high in 1993 (8 of 10 (80 percent) known owl pairs nested), low in 1994 and 1995 (1 of 13 (8 percent) and 4 of 15 (27 percent) known pairs nested, respectively) and moderate in 1996 (10 of 22 (45 percent) known pairs nested).

Behavior Prior to Dispersal

Juveniles typically fledged during the first few weeks of June. They generally roosted within 50 m of one or both parents for about 2 months after fledging (27 of 29 (93 percent) roosts prior to August 15, n = 3 individuals) and then only seldomly roosted within 50 m of one or both parents during the month prior to dispersal (4 of 24 (17 percent) roosts after August 15, n = 3 individuals). Sibling pairs usually roosted in the same tree as each other, or within close proximity (< 50 m; 33 of 43 (77 percent) roosts, n = 4 pairs), until just prior to dispersal.

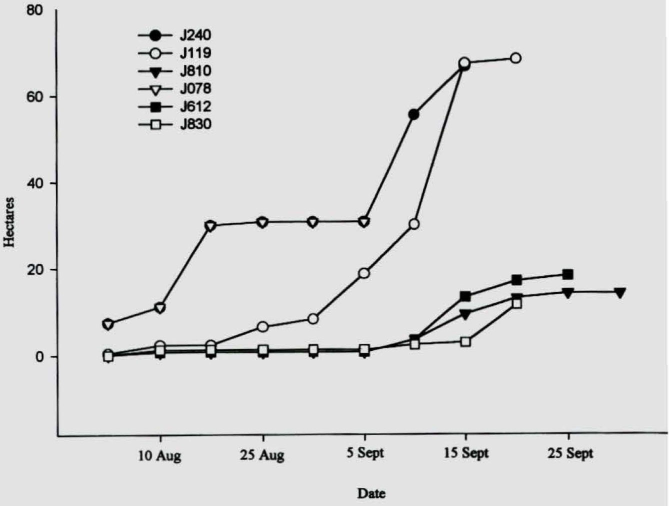

Figure 2.—*Change in the total area used by juvenile Mexican Spotted Owls in New Mexico prior to dispersal.*

The mean observed home range size of juveniles before dispersal was 61.8 ha (n = 7, range = 11.5 - 223.0 ha; table 1), considerably less than the area used by adults. The minimum mean home range size of four adult pairs radio-tagged in the San Mateos was 261.4 ha, calculated from data collected only during the breeding season. Other studies of the Mexican Spotted Owl report home range sizes of 381 to 1551 ha (p. 27, USDI 1995). The area used by juveniles increases sharply in September, just prior to dispersal from the natal area (fig. 2). All radio tagged juveniles are known to have survived to disperse except for J630 which dropped its transmitter in its natal area sometime before December 14, 1996. This juvenile was located on the edge of its parents territory on September 21, prior to which it used a home range of 24.3 ha. J630 was not detected anywhere after September 21, 3 days after its sibling J830 had dispersed, until it was found back on the natal area again on September 28. Apparently this juvenile had made an exploratory move and then returned to its natal territory, although the extent of this move is

Table 1.—*Dispersal dates of juvenile Mexican Spotted Owls in New Mexico.*

Owl	Last date located in natal area	Date known to have dispersed	Home range size (ha) prior to dispersal	Days between dispersal of siblings
1993				
J430[1]	August 24	September 10	NA	8-23
J078[2]	September 10	September 11	30.6	5-7
J240[2]	September 15	September 18	66.7	5-7
J449[1]	September 16	September 23	NA	8-23
J119	September 21	September 25	68.3	No sibling
1996				
J571[3]	August 14	September 10	NA	4-30
J689[3]	September 13	September 15	NA	4-30
J670	September 13	September 15	NA	No sibling
J830[4]	September 17	September 19	11.5	16-?
J612[5]	September 25	September 26	18.1	3
J810[5]	September 28	September 29	14.1	3
J630[4]	October 3	Unknown[6]	223.0	16-?
			61.8 (mean)	

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[1] Water Spring siblings.
[2] Apache siblings.
[3] Taylor Cabin siblings.
[4] Limestone siblings.
[5] Escondido siblings.
[6] Transmitter dropped in natal area sometime before December 3, 1996

unknown. J630 remained in the vicinity of its natal area until at least October 3, during which time its home range size increased to 223 ha (fig. 3). After this time its fate is unknown. Our observations suggest that juvenile Mexican Spotted Owl dispersal is preceded by a sudden increase in home range as well as by siblings roosting apart more frequently.

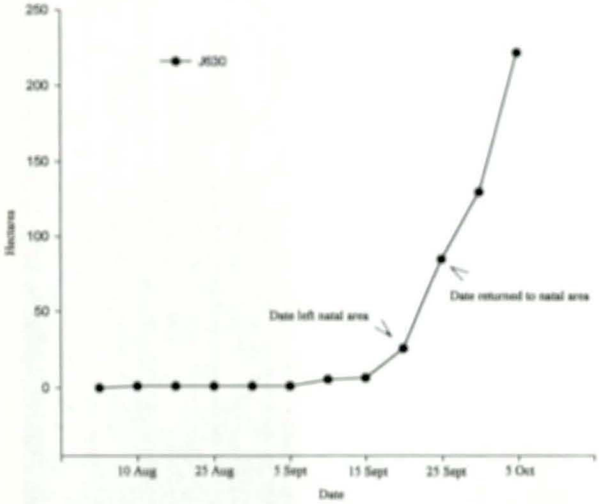

Figure 3.—*Change in the total area used by J630 before and after its exploratory move away from the natal area in New Mexico.*

Juvenile Dispersal

Nine of the 12 juveniles are known to have dispersed from September 10 to September 29 (table 1); two (J430 and J571) dispersed either during late August or early September (table 1). The length of time that elapsed between the dispersal of siblings was 3 to more than 15 days (table 1). Once juveniles dispersed from their natal areas they moved rapidly across the landscape. In their first week of dispersal, juveniles moved from 9.7 to 44.8 km traveling up to 11.3 km in 1 day (table 2). Juveniles were observed traveling through up to three occupied owl territories in 1 night.

After these initial rapid movements juveniles were observed remaining in the area they had traveled to for 3 to 16 days, before making subsequent long-distance movements. One juvenile (J612) moved 14.5 km southeast from its natal area in its first 2 nights of dispersal. Thereafter it remained in the same area for at least 1 week. This juvenile's transmitter was found on the ground in December, 22.5 km south of its last known location (fig. 4). Another juvenile (J689) moved 11.3 km east to Stiver Well in the first 2 nights after leaving its natal area. This juvenile remained in this area for 3 days, made a second movement of 11.1 km to Mineral Creek where it remained for 4 days, and then returned to Stiver Well for another 6 days. J689 then moved 6.4 km southeast, where it stayed for 1 day before disappearing. This juvenile was found December 18, 22 km southeast of its last known location (fig. 4). A third juvenile (J571) moved 12.9 km from its natal area to Diamond Creek, where it remained for 16 days before continuing to disperse four more km southwest to a location where it dropped its transmitter (fig. 4). In summary, juveniles exhibited two types of dispersal behavior, moving rapidly across the landscape and extensive local exploration.

The mean straight line distance that juveniles were observed moving from their nest site to their last known location was 21.8 km, and ranged from 1.3 km (J630 which dropped its transmitter in its natal area) to 57.6 km (table 3). Five juveniles dropped their radio transmitters, six juveniles were "lost" (undetected) 35 to 331 days (mean = 100) after their transmitters were attached and one juvenile's location was known as of the last telemetry

Table 2.—*Distances moved by juvenile Mexican Spotted Owls in the first week of dispersal from their natal areas in New Mexico.*

Owl	Greatest distance observed moving in one night (km)	Total distance moved during first week of dispersal (km)	Average distance moved per night during first week of dispersal (km)
J689	11.3	19.4	2.8
J119	11.2	44.8	11.2 (4 days)
J810	10.5	14.5	7.3 (2 days)
J612	8.9	16.3	2.3
J830	3.8	26.6	3.8

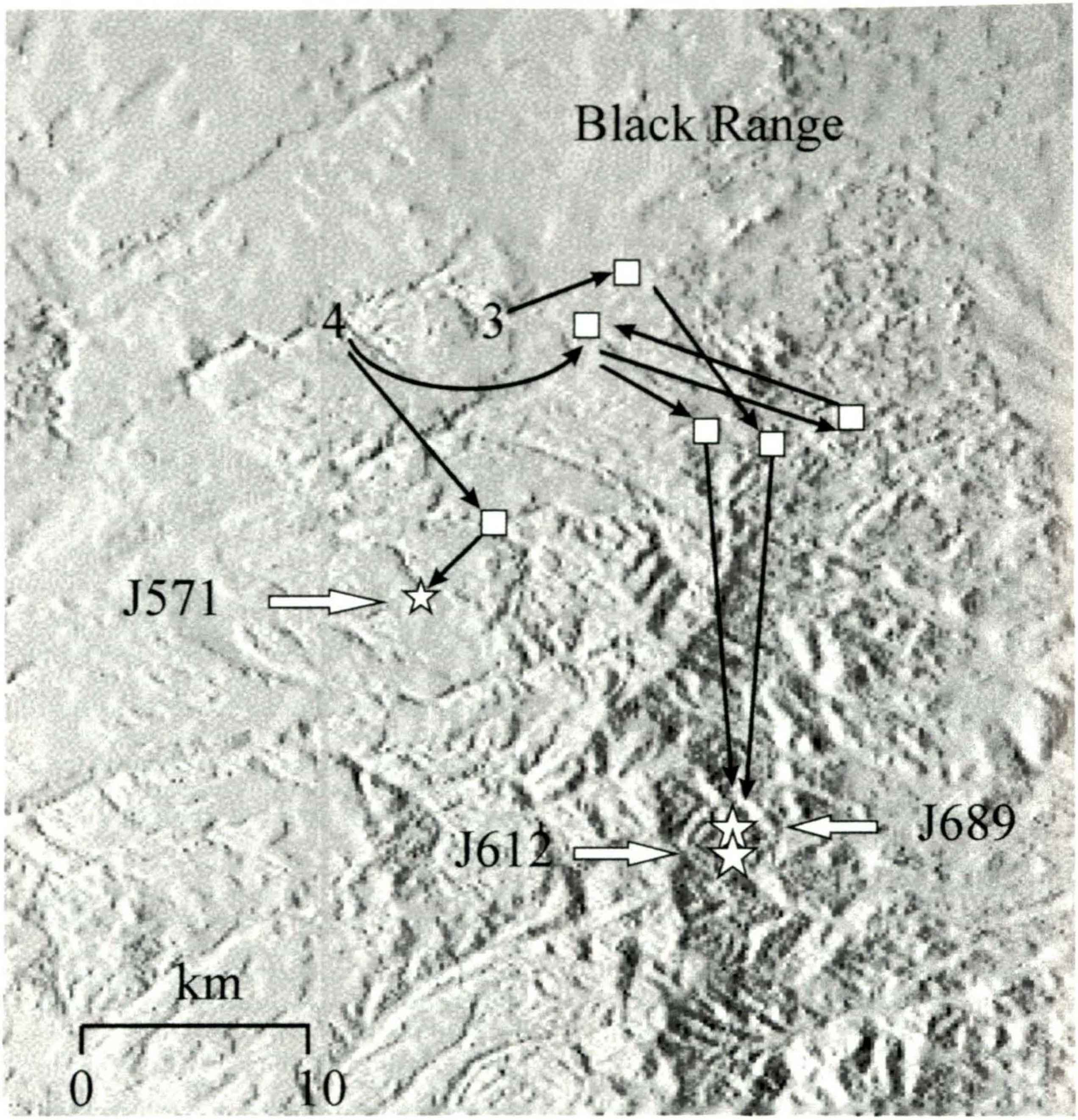

Figure 4.—*Dispersal of three juvenile Mexican Spotted Owls in the Black Range, New Mexico. Natal areas indicated by numbers: 3 = J612, and 4 = J571 and J689.* ☐ *= locations of dispersing juveniles.* ☆ *= last known locations of dispersing juveniles.*

flight on December 18, 1996 (table 3). Five juveniles were observed moving only within the San Mateo Mountains and five juveniles were observed moving only within the Black Range. Two juveniles crossed 20-40 km of grassland and pinon/juniper savanna habitat from the San Mateo Mountains to the Black Range. One of these juveniles (J119) flew 44.8 km from the San Mateo Mountains to the Black Range in only 4 days, thus moving a minimum of 11.2 km/night (fig. 5). The other (J430) first moved within the San Mateo Mountains 15 km southwest of its natal area. Subsequently this juvenile moved 31 km southeast to the northern Black Range. A second, and final, location for this juvenile in the Black Range was obtained 22 km south of the previous location (fig. 5).

Table 3.—*Observed dispersal distances by juvenile Mexican Spotted Owls in New Mexico.*

Owl	Date radio-tagged	Last date detected	Straight line distance (km) to last known location	Status
J630	08/02/96	10/03/96 (62 days)[1]	1.3	Dropped transmitter
J240	07/03/93	11/16/93 (135 days)	6.8	Undetected
J670	07/26/96	09/30/96 (65 days)	8.4	Dropped transmitter
J078	07/02/93	11/16/93 (136 days)	11.6	Undetected
J810	07/23/96	09/30/96 (68 days)	15.5	Undetected
J571	08/10/96	09/30/96 (51 days)	18.0	Dropped transmitter
J449	08/05/93	07/01/94 (331 days)	18.4	Dropped transmitter
J830	08/02/96	09/30/96 (59 days)	25.0	Dropped transmitter
J612	08/07/96	10/04/96 (58 days)	32.0	Dropped transmitter
J689	07/24/96	12/18/96 (146 days)	32.2	Detected last effort
J119	08/21/93	09/25/93 (35 days)	44.8	Undetected
J430	08/05/93	09/26/93 (52 days)	57.6	Undetected
Mean		(99.8 days)	22.6	

[1] Number of days between date transmitted and last date detected.

Juveniles were found roosting in habitat unlike that normally used by adults. Five of the seven juveniles radio tagged in 1996 were observed roosting in open ponderosa pine forest on several occasions prior to and during dispersal. Another juvenile (J449) was found November 17 roosting on the ground under a pinon tree near the top of a dry, west facing slope of pinon/juniper woodland. This juvenile was found again in July 1994. It had moved within the same drainage from a lower elevation site (2,256 m), with little canopy closure, to a higher elevation site (2,658 m) with greater canopy closure.

Transects were flown over the Black Range and San Mateo Mountains during two telemetry flights in September and November 1993, one in March 1994, one in March 1996 and three in September and December 1996. No juveniles have been tracked from birth site to first breeding site so natal dispersal has not been documented. In our entire study of spotted owl demography in New Mexico, no banded juveniles (n = 36) have been observed breeding. No radio-tagged juveniles have been found dead.

Sub-adult Dispersal

Observations of sub-adults were from three owls in 1994 and one in 1995. Early in the breeding season, three radio-tagged sub-adults were paired with adult males and were found regularly roosting with their males from May through July, however pairs were not observed attempting to breed. In August, pairs began roosting apart, with the adult males remaining within the established territory and sub-adult females roosting up to 9 km from the roosting area of their mate. Two sub-adults roosted 9 km and 5 km from their mates, and then returned to roost with them for approximately 2 weeks before leaving the territory again. At the end of September these two sub-adults could no longer be located during ground searches of the surrounding vicinity. The third sub-adult female also made forays of up to 4 km from the roosting area of the adult male during August and September. The following April, after an extensive ground search, this sub-adult also was not located and its previous mate had paired with a new adult female.

A female radio-tagged as a juvenile (J449) in 1993 was also observed as a sub-adult in 1994. She had moved 18.4 km from her natal area to a location near a spring at 2,800 m elevation within spruce-fir habitat. This location was higher in elevation than any other owl we have located and could be considered sub-optimal. She stayed in this area for the summer and was not located there in 1995.

DISCUSSION

The number of Mexican Spotted Owl pairs attempting to breed in our study area varied greatly from year to year (from 8 to 80 percent). High reproductive variance has also been

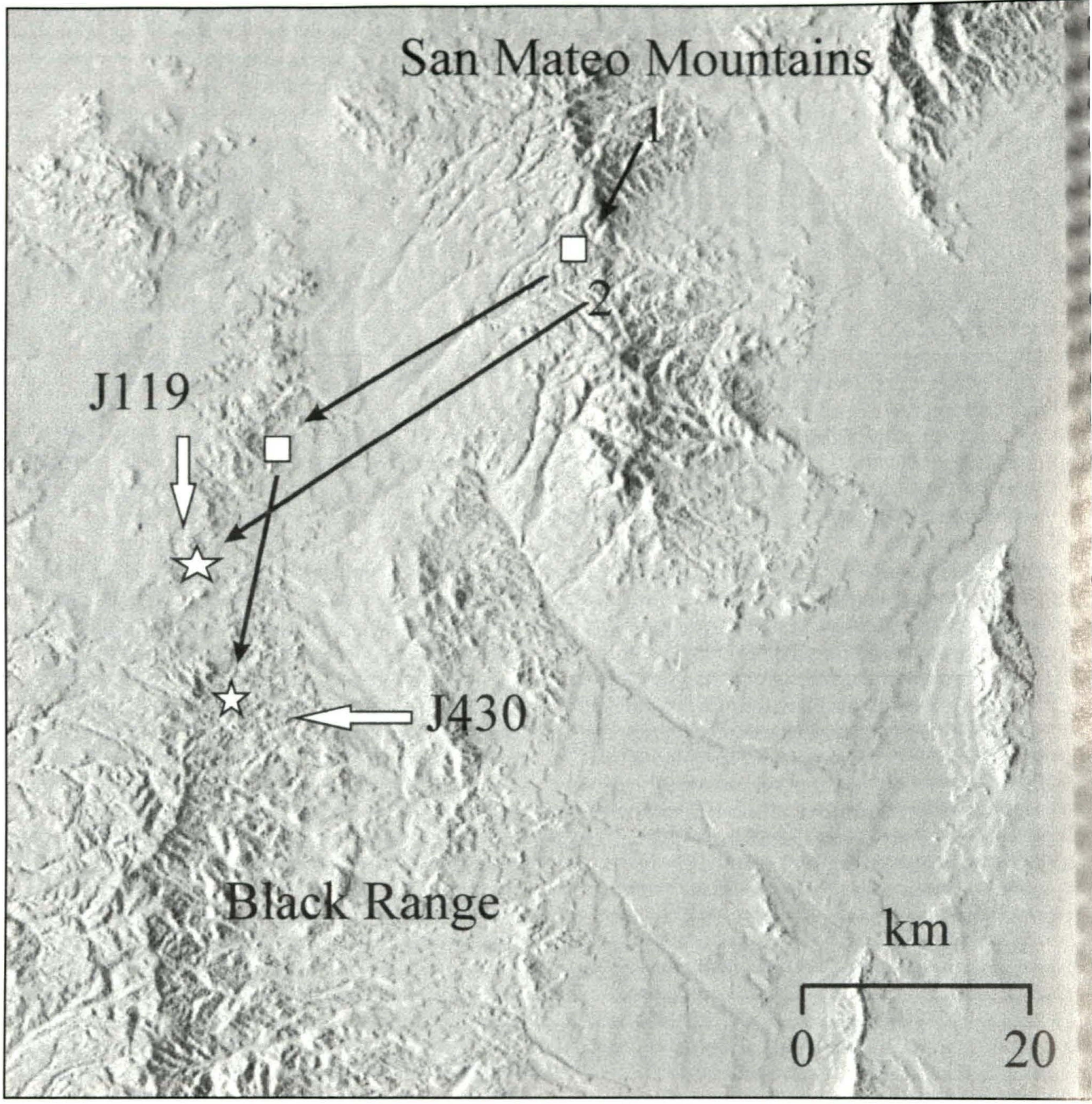

Figure 5.—*Dispersal of two juvenile Mexican Spotted Owls from the San Mateo Mountains to the Black Range, New Mexico. Natal areas indicated by numbers: 1= J430, and 2= J119.*☐*= locations of dispersing juveniles.* ☆*= last known locations of dispersing juveniles.*

observed in the Northern Spotted Owl (*S.O. caurina*) (from 14 to 89 percent of pairs attempting to breed; Forsman *et al.* 1984, Miller 1989) and the California Spotted Owl (S.O. *occidentalis*) (Gutierrez *et al.* 1985). Demographic models predict that small populations with high variance in reproductive success, such as the spotted owl, should quickly go extinct unless individuals disperse between isolated populations, thus forming a metapopulation (e.g., Stacey and Taper 1992, Stacey *et al.* 1997). This may be true of spotted owl populations in the southwest U.S. which are often small and restricted to isolated mountain ranges. We observed two individuals which dispersed from the San Mateo

Mountains across 20-40 km of unsuitable habitat to the Black Range. These types of dispersal events may be fairly common in the southwest U.S., connecting otherwise isolated mountain ranges which together may function as a metapopulation.

The Recovery Plan for the Mexican Spotted Owl (USDI Fish and Wildlife Service 1995) determined that nearly all isolated habitat patches defined as mixed conifer or ponderosa pine (although not preferred Mexican Spotted Owl habitat) in New Mexico, and throughout the Southwest, could be reached if an owl could disperse at least 60 km between isolated habitat patches. The movement distances of juvenile Spotted Owls given in the literature and the findings of this study indicate that Mexican Spotted Owls are capable of dispersing between nearly all isolated habitat patches in New Mexico and the Southwest. Whether they do or not is unknown except for our observations of juveniles moving between the Black Range and San Mateo Mountains in southwestern New Mexico.

Juvenile Mexican Spotted Owls most likely disperse far greater distances than we were able to detect during this study. Of 36 juveniles banded we have not resighted or recaptured any of them in other mountain ranges. This suggests that either juveniles are not detected as adults (unlikely if breeding), they die, or they move beyond our study area. The distances we observed dispersing radio-marked juveniles moving was 1.3 km to 57.6 km, similar to what other studies have reported (22 to 145 km for the Mexican Spotted Owl: p. 33 USDI Fish and Wildlife Service 1995, Gutierrez *et al.* 1996; 22 to 99 km for the California Spotted Owl: Gutierrez *et al.* 1985; and 3.2 to 78 km for the Northern Spotted Owl: Miller 1989). However, these numbers are only distances to the last known location of juveniles and not actual natal dispersal distances. In a technical assessment of the California Spotted Owl (Verner *et al.* 1992), the results of all radio-tracking studies of dispersing juvenile Northern and California Spotted Owls were compiled and only one juvenile out of 56 was ever found as a member of a mated pair, but it never nested. Sixty-eight percent of the juveniles died, 27 percent of their transmitters failed and 5 percent disappeared. Furthermore, our observations of sub-adult movements indicate that dispersal may continue into some spotted owls' second year making radio-tracking to breeding sites even more challenging. These difficulties make the observation of natal dispersal to a first breeding site difficult and rare.

The most recent demographic models being used to predict the viability of the spotted owl are spatially defined, considering dispersal both within and between clusters of suitable habitat to simulate fragmentation and predict optimal reserve designs (Doak 1989; Lamberson *et al.* 1992, 1994). Many of these models incorporate the ideas presented by Murray (1967) that competition for resources determines dispersal distance and individuals are most likely to settle on the first available breeding site they encounter. In these models a juvenile first searches her (only females are considered) natal cluster for an available site and if she is not successful is forced to disperse between clusters. Our results indicate that juvenile owls seem not only to be very efficient at searching the landscape (moving through up to three owl territories and up to 11.3 km in one night), but they also appear to keep moving past suitable and currently unoccupied spotted owl territories. Additionally, J119 was observed crossing over at least 25 km of unsuitable habitat between the Black Range and San Mateo Mountains moving a distance of 44.8 km in less than 4 days after dispersing from its natal area. This owl apparently did not search for available habitat in the San Mateo Mountains, but rather moved immediately to a new mountain range. Furthermore, if juveniles chose to occupy the available habitat around their natal areas we would expect that more banded juveniles would be found nesting within large study areas, yet in New Mexico these instances are rare. These observations suggest that juvenile spotted owls may not settle on the first available and suitable location they find, because of a tendency to continue dispersal, and that their ability to search the landscape may be very efficient. This type of juvenile search pattern should be included in any future model of population viability for the Mexican Spotted Owl in the Southwest.

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LITERATURE CITED

Bendire, C.E. 1892. Life histories of North American birds. U.S. National Museum. Special Bulletin 1.

Brookes, M.I.; Butlin, R.K. 1994. Population structure in the small ermine moth *Yponomeuta padellus*: an estimate of male dispersal. Ecological Entomology. 19: 97-107.

Dick-Peddie, William A. 1993. New Mexico vegetation, past, present and future. Albuquerque, NM: University of New Mexico Press.

Doak, D. 1989. Spotted Owls and old growth logging in the Pacific Northwest. Conservation Biology. 3: 389-396.

Forsman. E.D. 1981. Molt of the Spotted Owl. Auk. 98: 735-742.

Forsman, E.D. 1983. Methods and materials for locating and studying Spotted Owls. Gen. Tech. Rep. PNW-162. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station.

Forsman, E.D.; Meslow, E.C.; Wight, H.M. 1984. Distribution and biology of the Spotted Owl in Oregon. Wildlife Monograph. 87: 1-64.

Ganey, J.L.; Balda, R.P. 1989. Distribution and habitat use of Mexican Spotted Owls in Arizona. Condor. 91: 355-361.

Gilpin, M.; Hanski, I. 1991. Metapopulation dynamics: empirical and theoretical investigations. San Diego, CA: Academic Press.

Greenwood, Paul J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Animal Behavior. 28: 1140-1162.

Gutierrez, R.J.; Seamans, M.E.; Peery, M.Z. 1996. Intermountain movement by Mexican Spotted Owls (*Strix occidentalis lucida*). Great Basin Naturalist. 56: 87-89.

Gutierrez, R.J.; Franklin, A.B.; LaHaye, W.; Meretsky, V.J.; Ward, J.P. 1985. Juvenile Spotted Owl dispersal in northwestern California: preliminary results. In: Gutierrez, R.J.; Carey, A.B., tech. eds. Ecology and management of the Spotted Owl in the Pacific Northwest. Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station: 60-65.

Hodgson, A.; Stacey, P.B. 1997. Habitat use of Mexican Spotted Owls in New Mexico. Submitted.

Lamberson, R.H.; McKelvey, K.; Noon, B.R.; Voss, C. 1992. The effects of varying dispersal capabilities on the population dynamics of the Northern Spotted Owl. Conservation Biology. 6: 505-512.

Lamberson, R.H.; Noon, B.R.; Voss, C.; McKelvey, K.S. 1994. Reserve design for territorial species: the effects of patch size and spacing on the viability of the Northern Spotted Owl. Conservation Biology. 8: 185-195.

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society of America. 15: 237-240.

Miller, G.S. 1989. Dispersal of juvenile Northern Spotted Owls in western Oregon. Corvallis, OR: Oregon State University. 139 p. M.S. thesis.

Murray, B.G. 1967. Dispersal in vertebrates. Ecology. 48: 975-978.

Phillips, A.R.: Marshall, J.T., Jr.; Monson, G. 1964. The birds of Arizona. Tucson, AZ: University of Arizona Press.

Seamans, M.E.; Gutierrez, R.J. 1995. Breeding habitat of the Mexican Spotted Owl in the Tularosa Mountains, New Mexico. Condor. 97: 944-952.

Slatkin, S. 1985. Gene flow in natural populations. Annual Review of Ecology Systematics. 16: 393-430.

Stacey, P.B.; Taper, M. 1992. Environmental variation and the persistence of small populations. Ecological Applications. 2: 18-29.

Stacey, P.B.; Johnson, V.A.; Taper, M.L. 1997. Migration within metapopulations: the impact upon local population dynamics. In: Hanski, I.; Gilpin, M., eds. Metapopulation biology: ecology, genetics and evolution. New York, NY: Academic Press: 267-291.

U.S. Department of Interior, Fish and Wildlife Service. 1995. Recovery plan for the Mexican Spotted Owl: Vol. I. Albuquerque, NM. 172 p.

Verner, J.; Gutierrez, R.J.; Gould, G.I., Jr. 1992. Chapter 4. The California Spotted Owl: general biology and ecological relations. In: Verner, J.; McKelvey, K.S.; Noon, B.R.; Gutierrez, R.J.; Gould, G.I., Jr.; Beck, T.W., tech. coords. The California Spotted Owl: a technical assessment of its current status. Gen. Tech. Rep. PSW-133. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. 285 p.

Woodhouse, S.W. 1853. Report on the natural history of the country passed over by the exploring expedition under the command of Brev. Capt. L. Sitgreaves, U.S. Topographical Engineers, during the year 1851. [and] Zoology. Birds. In: Sitgreaves, Capt. L., ed. Report of an expedition down the Zuni and Colorado Rivers. Washington, DC: Robert Armstrong, Public Printer: 33-40, 58-105.

Wright, S. 1951. The genetical structure of populations. Ann. Eugenics. 15: 323-354.

Zink, R.M.; Dittman, D.L. 1993. Gene flow, refugia, and evolution of geographic variation in the Song Sparrow (*Melospiza melodia*). Evolution. 47: 717-729.

Barn Owl (*Tyto alba*) and Long-eared Owl (*Asio otus*) Mortality Along Motorways in Bourgogne-Champagne: Report and Suggestions

Hugues Baudvin[1]

The purpose of the study was to find where and why two species of owls were killed by traffic along motorways. Three different factors have an important influence on the mortality of the two owl species: the biotops crossed by motorways, the road elevation and the presence of small rodents, the Common Vole (*Microtus arvalis*) being most numerous. In order to limit the mortality caused by motorways, it is proposed to let the bordering vegetation grow naturally.

Roadway-caused mortality of wildlife is a significant issue worldwide. Often, the impacts to wildlife occur along specific portions of roadways. Surveys along the roadways can identify these portions and identify the wildlife species being the most greatly impacted. Then, the management of roadside vegetation can help to reduce this negative impact.

STUDY AREA AND METHODS

The study area is located in the northeast of France, over the regions of Burgundy, Champagne, and Lorraine (fig. 1). It concerns 305 km of motorways, from Dijon (Burgundy) to Toul (Lorraine) and from Dijon to Saint-Thibault (Champagne). Because of lack of data, 46.1 km of road were not evaluated (discontinuous line figure 2). The distance studied is exactly 517.8 km (258.9 x 2 sides of the motorway). The study was conducted from November 1991 to December 1995. Dead animals were collected systematically along the motorway three times daily. The animals were placed in plastic bags and frozen for positive identification. Detailed notes were taken denoting the date, species, and specific location along the motorway where the animals were found. Measurements were also made on the length and weight of the animals, as well as on their sex, age, and stomach contents. The roadway crossed four major biotypes including forests, cereal fields, meadows, and sand pits. These biotops were subsequently divided into 100 or 500 m segments depending on the number of victims.

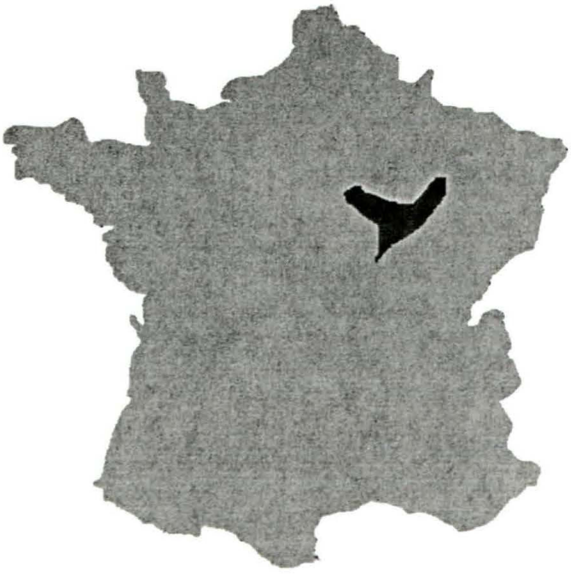

Figure 1.—*Study area (black), in the northeast of France, over the regions of Burgundy, Champagne, and Lorraine.*

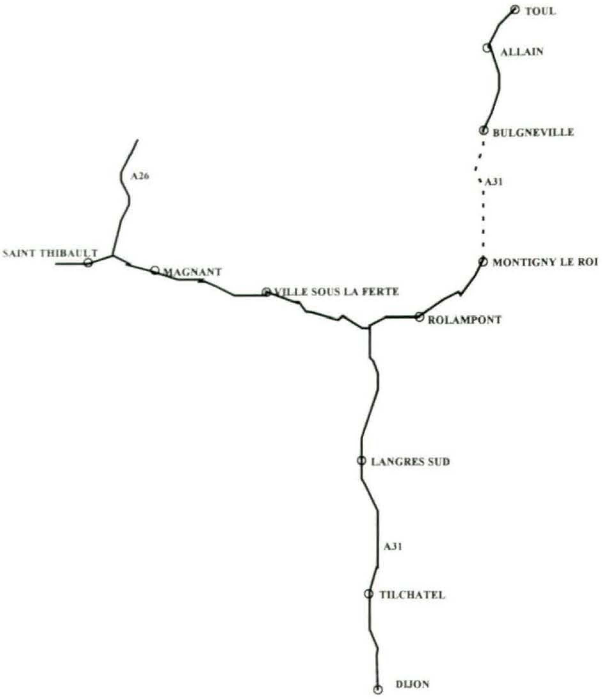

Figure 2.—*Owl mortality on motorways studied in northeastern France.*

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[1] La Choue, Lignière, 21350 Beurizot, France.

RESULTS

Twenty-two mammal and reptile species (table 1) and 46 bird species (table 2) were collected. Carnivores represented 82.5 percent of the mammals and owls and diurnal raptors accounted for 81.5 percent of the birds. The Barn Owl (*Tyto alba*) and the Long-eared Owl (*Asio otus*) were the birds most killed by the motorway traffic. Most notably, the predators of small rodents were disproportionately represented in the sample of the animals collected. In part, this is due to the situation where roadway margins were providing the grassland habitat which supported high numbers of voles.

Table 1.—*Mammal and reptile species collected along motorways studied in northeastern France.*

Mammals	**Total**
Felis sylvestris	434
Domestic cat	109
Vulpes vulpes	415
Meles meles	50
Martes martes	100
Martes foina	61
Martes sp.	150
Putorius putorius	17
Mustela erminea	4
Mustela nivalis	2
Lepus capensis	36
Oryctolagus cuniculus	24
Lepus/*Oryctolagus*	168
Sciurus vulgaris	18
Myocastor coypus	14
Ondatra zibethicus	3
Rattus sp.	19
Arvicola terrestris	1
Total	1,625

Other “prey”	
Capreolus capreolus	42
Sus scrofa	3
Domestic pig	3
Dog	7
Erinaceus europaeus	316
Snake	3
Total	374

Table 2.—*Bird species collected along motorways studied in northeastern France.*

Birds	**Total**
Tyto alba	674
Asio otus	300
Strix aluco	53
Athene noctua	1
Buteo buteo	213
Falco tinnunculus	48
Falco columbarius	1
Milvus milvus	7
Milvus migrans	2
Accipiter gentilis	1
Accipiter nisus	1
Phasianus colchicus	51
Perdix perdix	77
Coturnix coturnix	2
Scolopax rusticola	1
Anas platyrhynchos	2
Ardea cinerea	1
Podiceps cristatus	1
Podiceps nigricollis	1
Gallinula chloropus	5
Fulica atra	4
Vanellus vanellus	19
Larus ridibundus	7
Rissa tridactyla	2
Alcedo athis	3
Pluvialis apricaria	1
Domestic hen	2
Domestic duck	1
Domestic pigeon	3
Carrier pigeon	10
Columba palumbus	7
Columba oenas	1
Columba sp.	18
Streptopelia decaocto	4
Streptopelia turtur	2
Corvus corone	23
Garrulus glandarius	6
Pica pica	1
Sturnus vulgaris	1
Turdus merula	26
Turdus philomelos	2
Turdus viscivorus	2
Turdus iliacus	1
Turdus sp.	2
Picus viridis	2
Caprimulgus europaeus	1
Cuculus canorus	1
Emberiza citrinella	2
Aves sp.	2
Total	1,598

The locations of Barn Owls and Long-eared Owls were analyzed, relative to the amount (i.e., availability) of roadway sections bordered by forests, cereal fields, meadows and sand pits. The owls were found along sections of roadway bordered by cereal fields in greater proportion to their availability and found along sections of roadway bordered by forests less than their availability (X^2 test $P < 0.05$, table 3).

The engineering of the roadway was also a factor contributing to owl mortality. The situation where the roadway surface was higher or at the same level of the bordering terrain was unfavorable to the owls. Many fewer owls were found in situations where the roadway surface was set below that of the surrounding terrain. (X^2 test $P < 0.05$ for the Barn Owl only, table 4).

Concerning the mortality of both owl species, the X^2 test shows a significant difference ($P < 0.05$) between the areas rich in voles and the poor ones (table 5).

CONCLUSION

It clearly appears that both species of owls are not just killed by crossing the motorway, but rather that they are attracted by the voles living in the borders. Not only do they take a risk when crossing the motorway perpendicularly, but also when flying along the route linearly in quest of small mammals. They are mostly hit by the vehicle's displacement of air and die of it or are incurably wounded (broken wing) and finished off by the following vehicles.

Table 3.—*The influence of the different biotops on the mortality of owls along motorways in northeastern France.*

Biotops	Distance		Barn Owl		Long-eared Owl	
	km	%	*n*	%	*n*	%
Forests	155.1	30.0	117	20.0	32	13.9
Cereal fields	251.4	48.5	356	60.9	165	71.8
Meadows	99.3	19.2	102	17.4	33	14.3
Sand pits	12	2.3	10	1.7	0	0.0
Total	517.8	100.0	585	100.0	230	100.0

Table 4.—*The influence of road elevation on the mortality of owls along motorways in northeastern France.*

Road elevation	Distance		Barn Owl		Long-eared Owl	
	km	%	*n*	%	*n*	%
Favorable	229.7	44.4	187	32.0	85	37.0
Not favorable	288.1	55.6	398	68.0	145	63.0
Total	517.8	100.0	585	100.0	230	100.0

Table 5.—*The influence of habitat (poor or rich in voles) on the mortality of owls along motorways in northeastern France.*

Voles habitat	Distance		Barn Owl		Long-eared Owl	
	km	%	*n*	%	*n*	%
Poor	257.3	49.7	154	26.3	58	25.2
Rich	260.5	50.3	431	73.7	172	74.8
Total	517.8	100.0	585	100.0	230	100.0

In order to reduce the Barn Owl's and the Long-eared Owl's mortality due to the motorways (and this may apply to roads in general) a solution consists in preventing the small rodents that live in immediate proximity from being reachable, either by letting the bordering vegetation grow naturally or by planting short bushes which would decrease prey availability and lead owls towards other areas which may be rich in prey, but surely less dangerous.

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Société des Autoroutes Paris-Rhin-Rhône
La Choue

Corticosterone and Dispersal in Western Screech-owls (*Otus kennicottii*)

James R. Belthoff and Alfred M. Dufty, Jr.[1]

Abstract.—Belthoff and Dufty (in press) posed a model for dispersal in screech-owls and similar nonmigratory birds. The model is based on interactions among hormonal changes, body condition, and locomotor activity patterns. It predicts that corticosterone increases in blood plasma prior to dispersal under endogenous and exogenous influences, and this increase mediates the locomotor activity that underlies dispersal. Juveniles in good body condition (i.e., those with sufficient fat reserves) will disperse at that time, while birds in poor body condition will not. The latter will increase their foraging activity under the influence of corticosterone and disperse later. This paper presents preliminary data that show that locomotor activity levels are reduced in captive Western Screech-owls at the time of dispersal under the influence of a corticosterone-blocking drug.

The objectives of this paper are to (1) review briefly a recent model that explains natal dispersal in birds, and (2) present results from a preliminary experiment that examines an important prediction of this model. Belthoff and Dufty (in press) proposed a theoretical model based upon interactions among hormonal changes, body condition, and locomotor activity patterns to explain dispersal in screech-owls and similar nonmigratory species of birds. Briefly, this model for dispersal predicts that corticosterone, an adrenal hormone known to stimulate locomotor activity and hyperphagia, increases in blood plasma prior to dispersal through endogenous and/or exogenous events. This increase in corticosterone mediates the locomotor activity that underlies dispersal, but it interacts with body condition such that juveniles in good body condition disperse first. Previous studies on Western and Eastern Screech-owls (*Otus kennicottii* and *O. asio*, respectively) have produced results that are consistent with the model, and these results are reviewed below. We also present results from a hormone manipulation study that examined the effect of a corticosterone blocker on locomotor activity in young Western Screech-owls at the time of dispersal.

NATAL DISPERSAL IN BIRDS

Dispersal is the movement of individuals from their point of origin (natal area) to where they reproduce or would have reproduced had they survived and mated (Howard 1960). Because these movements are characteristic of individuals in the juvenile age class and they represent departures from the natal area, Greenwood (1980) later coined the term *natal dispersal* to describe them. Virtually all species of birds make a dispersal movement at some stage of the life cycle, and juveniles of both sexes usually disperse from parental territories soon after they achieve independence during the post-fledging period (e.g., Belthoff and Ritchison 1989).

Several aspects of the dispersal process are of interest to students of the ecology of animal movement. These include the initiation of dispersal and its timing, distance, duration, rate, and direction of movements, and the effectiveness of the movement (i.e., whether the bird survived dispersal and successfully reproduced in the new area). Certainly, each of these components of dispersal could come under selection, but the dispersal model developed by Belthoff and Dufty (in press) relates primarily to the first of these, the initiation of dispersal and its timing.

Beyond achieving independence from adults, the proximate factors that stimulate young to initiate dispersal are poorly understood. Some factors that may be important are parental aggression toward young, aggression of young toward each other, and resource depletion within the natal area (e.g., De Laet 1985, Kenward and others 1993, Wiggett and Boag 1993). Despite evidence that such exogenous factors are important in driving dispersal, some birds disperse even though their parents have been removed and they have unlimited access to food (Nilsson 1990). In these cases, dispersal must have been initiated by some endogenous mechanism. Endogenous mechanisms likely involve hormones, they appear to be influenced by the body condition of the individual, and ontogenetic effects are most certainly involved, such that the movement occurs at the biologically appropriate time (Belthoff and Dufty in press, Holekamp 1986, Holekamp *et al.* 1984).

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At least for many nonmigratory species, one factor appears relatively clear: selection has operated for dispersal to occur early so that it is usually initiated and completed before winter (Morton 1992). If territories are at a premium, selection might also operate on young to disperse as early as they can, and this may be particularly important in resident species that defend territories the year round. Many migratory species do not establish territories until the subsequent breeding season; therefore they may not be under identical selection pressures, and this is why the dispersal model is specific to nonmigratory species. However, it probably has important applications to dispersal in migratory species of birds as well (Belthoff and Dufty in press).

THE BELTHOFF AND DUFTY DISPERSAL MODEL

Belthoff and Dufty (in press) hypothesized that avian dispersal is influenced by the adrenal hormone corticosterone. The model argues that as the post-fledging period progresses, parents reduce their provisioning of young and/or competition increases among siblings. Any resulting reduction in food intake by juveniles causes stress, or endogenous pathways are triggered at the biologically appropriate time, and either or both increase adrenal activity, leading to increased secretion of corticosterone. Increased plasma corticosterone levels stimulate or are accompanied by increased locomotor activity. The model suggests further that corticosterone levels interact with body condition to induce dispersal. When corticosterone secretion increases, activity levels increase, and this eventually leads young to disperse. However, only those juveniles that are in good physical condition are prepared for immediate dispersal. That is, only juveniles with the necessary fat stores will survive the rigors of territory establishment, territory defense and independent foraging. Good physical condition includes adequate lipid reserves, and this provides a buffer against possible corticosterone-induced depletion of muscle tissue. On the other hand, juveniles in poor condition at the time that plasma corticosterone levels increase will require more time to forage in the natal area to attain the physical condition necessary to disperse successfully. The model predicts that corticosterone levels remain elevated in these birds, stimulating increased foraging behavior that improves body condition and, eventually, promotes dispersal. Following dispersal of their siblings in better condition, the remaining juveniles undergo reduced competition for food, they experience less aggression from siblings, and they have the exclusive attention of the parents. This improves their physical condition and eventually leads to natal dispersal. Thus, the model predicts a relationship between physical condition, the extent to which corticosterone levels remain elevated, and the timing of natal dispersal, such that birds in good physical condition leave the natal area first.

STUDY SPECIES

The dispersal model (Belthoff and Dufty in press) is based upon the biology of two representative species of nonmigratory birds: Eastern and Western Screech-owls. These owls are common to eastern and western North America, respectively, and sufficient data are now available from both field and laboratory studies to begin to understand factors affecting their dispersal behavior. The post-fledging behavior and dispersal of radio-tagged Eastern Screech-owls in Kentucky was described by Belthoff and Ritchison (1989, 1990), Ritchison *et al.* (1992), Belthoff *et al.* (1993), and Sparks *et al.* (1994). Briefly, young screech-owls fledge in mid-May and spend roughly the next 5 weeks in close association with adults. After this time, young increase their independence from adults by roosting farther away, increasing the sizes of their home ranges, and wandering outside the nightly ranges of their parents more frequently. During this same time period, locomotor activity levels of both captive and free-living owls are high. Young owls of both sexes initiate dispersal approximately 8 weeks after fledging, usually in mid-July, although the timing of dispersal within and among broods varies. Many of the dispersing owls settle in overwinter sites between 1 and 17 km from the natal area. The number of birds for which suitable data are available is small, but individuals settle an average of approximately 6 days after initiating dispersal, and some individuals breed in or near these overwinter sites. Studies by Belthoff and Dufty (1995, in press) and Ellsworth and Belthoff (unpubl. data) suggest that the post-fledging behavior and dispersal of Western Screech-owls is similar to that of their eastern counterpart. Because of these similarities, Belthoff and Dufty (in press) believe that their model is applicable to both species of screech-owls, as well as to other similar species of birds.

SUPPORTIVE DATA

Body Condition and Dispersal

Initial results have been consistent with the dispersal model (Belthoff and Dufty in press). For example, one prediction of the model is that individuals in adequate body condition will disperse when corticosterone levels increase. Individuals in poorer body condition will continue to forage on the natal area and disperse later. There have been no direct tests of the effects of body condition on the dispersal of screech-owls. However, Ellsworth and Belthoff (unpubl. data) have examined effects of social dominance on the timing of dispersal in young Western Screech-owls. This study used video cameras to record dominance interactions among nestlings, and followed radio-tagged young during the post-fledging period and as they dispersed. Individuals scored as dominant were the first to disperse in six of the seven broods. Moreover, the most subordinate juvenile dispersed last in five of seven broods. Finally, in four broods, the order of dispersal correlated perfectly with dominance status, even in a brood with as many as five young. If dominance status is a predictor of body condition in these young, and assuming dominant birds have the best body condition, then these data indicate that young in good condition dispersed earlier, and they provide at least indirect support for the body condition prediction of the model (Belthoff and Dufty in press).

Locomotor Activity and Dispersal

The model also predicts that locomotor activity levels should be high or peak near the time of dispersal, and this prediction has been supported in studies by Ritchison *et al.* (1992) and Belthoff and Dufty (1995). For example, both captive and free-living screech-owls show increased locomotor activity at the time of dispersal, and they exhibit much lower activity thereafter (Ritchison *et al.* 1992, Belthoff and Dufty 1995).

Plasma Corticosterone and Dispersal

Finally, Belthoff and Dufty (in press) reported that circulating corticosterone levels in captive Western Screech-owls were elevated before or during the time when locomotor activity was greatest. Plasma corticosterone levels were high or peaked during the period of greatest locomotor activity, and corticosterone levels were almost always lower outside of this period (Belthoff and Dufty in press). One interesting result was that corticosterone often peaked around 35-40 ng/ml, which is equivalent to maximum circulating corticosterone levels exhibited by many passerines during the migration period (e.g., see Holberton *et al.* 1996). This is of particular interest because it indicates that some of the physiological mechanisms underlying dispersal and migration may be similar.

While these results illustrate an association between corticosterone and locomotor activity at the time of dispersal in Western Screech-owls, they do not allow confirmation of cause-effect relationships between these two variables. Experiments that manipulate either or both of these variables are required before such relationships can be understood completely.

HORMONE MANIPULATION EXPERIMENT

To begin to understand the cause-effect relationships between corticosterone and locomotor activity at the time of dispersal, we performed a hormone manipulation study on captive Western Screech-owls using metyrapone, an 11*B*-hydroxylase inhibitor that reduces the production of adrenal corticosteroid hormones, including corticosterone (Jain *et al.* 1993, Zulkifli *et al.* 1993). If corticosterone is important in the initiation or maintenance of locomotor activity at the time of dispersal, birds exposed to metyrapone are expected to show reduced locomotor activity compared to control owls which receive only a placebo, or metyrapone-treated owls should fail to show the typical peak in activity that occurs in captive owls near the time of dispersal.

In July 1996, which corresponds to the dispersal period for Western Screech-owls in Idaho (Ellsworth and Belthoff, unpubl. data), we treated four young Western Screech-owls with subcutaneous implants of metyrapone (90-day release, 10 mg total dosage capsule, Innovative Research of America, Toledo, OH) and monitored the owls' locomotor activity for the next 5 weeks. These birds had been collected from the wild as nestlings (approximately 1 week prior to fledging) and maintained in captivity in wire mesh cages and isolation chambers similar to those described by Belthoff and Dufty (1995) and Dufty and Belthoff (1997). Four other birds were housed in a similar fashion but were treated with a placebo rather than the drug, and they served as controls. Locomotor activity in relation to the hormone manipulation was monitored using digital pedometers (Micronta Mini Jog-Mate pedometers, Cat. No. 63-667, Radio Shack, Fort Worth, TX) attached to the backs of owls which registered the number of hops each owl made over a 24 hour period (see Ritchison *et al.* 1992, Belthoff and Dufty 1995, in press for specifics on pedometers and their attachment). Complete packages, i.e., pedometers plus nylon cord, weighed approximately 9 g, which was equivalent to approximately 5 percent of each individual's body weight. Activity levels were recorded daily at 1600 h, and individual activity levels were averaged to obtain weekly scores. Using repeated measures analysis of variance (2 x 5 mixed factorial design), these weekly averages were analyzed to assess the null hypothesis that activity levels of treatment and control owls did not differ. Separate analyses were performed on activity levels (hops registered from pedometers) and percentage change from activity levels during the week prior to the treatment (percentage difference in average activity level).

Figure 1 shows the activity data from the metyrapone-treated and control birds as a function of weeks after they received the implant. Activity levels differed by week ($F_{4,24}$ = 5.97, P = 0.002), but there also was an effect of the treatment; birds treated with metyrapone had lower activity levels than control birds ($F_{1,6}$ = 5.17, P = 0.063). Finally, there was no treatment by week interaction ($F_{4,24}$ = 1.14, P = 0.360). The lack of a significant interaction indicates that birds treated with metyrapone had lower activity levels than control birds across all weeks of the experiment (fig. 1). Birds in the control group also exhibited a highly significant increase (P = 0.0097) in average activity levels between week one and two following the treatment (fig. 1); this increase resembles the peak in activity at the time of dispersal observed in previous experiments with screech-owls (e.g., Ritchison *et al.* 1992, Belthoff and Dufty 1995). There was a much smaller increase (P = 0.0618) in average activity levels between weeks one and two after the treatment for owls in the metyrapone group (fig. 1). These results are consistent with the notion that metyrapone dampened increases in activity levels at the time of dispersal.

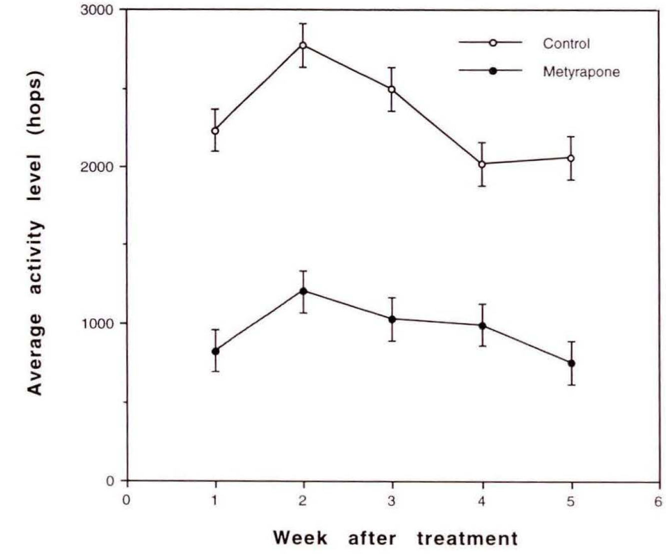

Figure 1.—*Average (± SE) locomotor activity levels at the typical time for dispersal in young Western Screech-owls exposed to metyrapone (N = 4) to reduce circulating corticosterone and control owls (N = 4) that received a placebo.*

One difficulty with examining only raw activity levels is that there can be inter-bird variation in initial activity levels that may account for some of the differences observed after application of the treatment. One way to control for such variation is to examine each owl's activity only in relation to its pre-treatment activity levels, which in effect standardizes the following activity readings to the initial ones. Thus, in a second analysis (fig. 2), we assessed the percentage change in activity following treatment as a function of the activity in the week before the treatment (e.g., [week before minus each week after]*100). Just as in the analysis of raw scores above, these measures differed significantly by week ($F_{4,24}$ = 11.88, P = 0.0001), and the metyrapone group had lower average values than the control birds ($F_{1,6}$ = 4.96, P = 0.068). There was no treatment by week interaction ($F_{4,24}$ = 1.70, P = 0.182). However, most of the difference between treatment groups was accounted for in weeks one and five after the treatment (fig. 2).

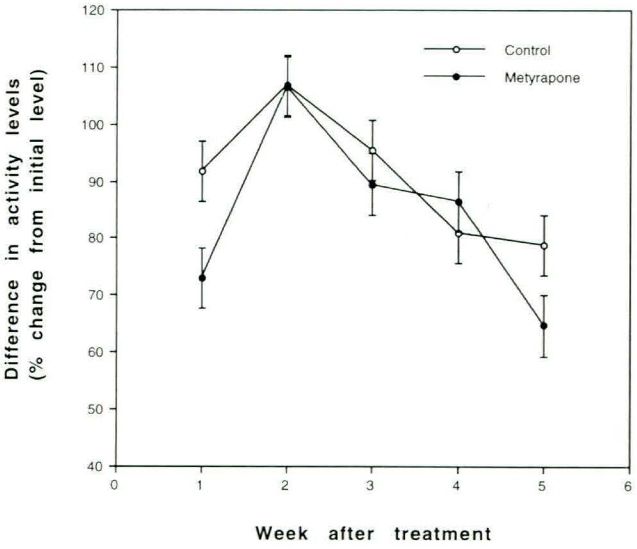

Figure 2.—*Locomotor activity levels expressed as average percentage change (± SE) from initial activity levels for Western Screech-owls that received metyrapone (N = 4) and control owls (N = 4) that received a placebo.*

The data from this initial experiment, at least in part, appear to be consistent with the predictions of the dispersal model. We predicted that if corticosterone stimulates locomotor activity, then treatment with a corticosterone blocker should reduce locomotor activity. The results suggest that activity levels of young birds at the time of dispersal may be affected by hormone manipulations, as birds that received metyrapone had lower activity levels than control owls.

SUMMARY AND CONCLUSIONS

In summary, we have proposed a model that examines the interplay between endogenous and exogenous factors that regulate natal dispersal in screech-owls and similar species of birds (Belthoff and Dufty in press). Initial results are generally in agreement with the model. Owls increase locomotor activity in the weeks leading up to dispersal, and this is accompanied by high circulating corticosterone in most cases. Also, owls in better body condition appear to be dispersing earlier. Results from an initial hormone manipulation experiment designed to reduce circulating corticosterone indicate that activity levels were significantly lower when owls received the drug treatment, and metyrapone may have dampened the peaks in activity levels normally seen in captive owls at the time of dispersal.

The model remains to be fully tested because cause-effect relationships between corticosterone and locomotor activity are only now being examined, and several variants of the model remain tenable (Belthoff and Dufty in press). Although it will be refined with future work, we believe that this model is an important first step in understanding the physiological ecology of dispersal in screech-owls and other non-migratory species of birds. Additional experiments that manipulate body condition, plasma corticosterone, and activity levels are underway as the next step in testing the model, and these should allow us to understand more fully the physiological ecology of dispersal.

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LITERATURE CITED

Belthoff, J.R.; Dufty, A.M., Jr. 1995. Locomotor activity levels and the dispersal of Western Screech-owls, *Otus kennicottii*. Animal Behaviour. 50: 558-561.

Belthoff, J.R.; Dufty, A.M., Jr. [1997.] Corticosterone, body condition, and locomotor activity: a model for natal dispersal in birds. Animal Behaviour. [In press.]

Belthoff, J.R.; Ritchison, G. 1989. Natal dispersal of Eastern Screech-owls. Condor. 91: 254-265.

Belthoff, J.R.; Ritchison, G. 1990. Roosting behavior of postfledging Eastern Screech-owls. Auk. 107: 567-579.

Belthoff, J.R.; Sparks, E.J.; Ritchison, G. 1993. Home ranges of adult and juvenile Eastern Screech-owls: size, seasonal variation and extent of overlap. Journal of Raptor Research. 27: 8-15.

De Laet, J.V. 1985. Dominance and aggression in juvenile Great Tits, *Parus major major* L. in relation to dispersal. In: Sibly, R.M.; Smith, R.H., eds. Behavioral ecology: ecological consequences of adaptive behavior. Oxford: Blackwell Scientific Publications: 375-380.

Dufty, A.M., Jr.; Belthoff, J.R. [1997]. Corticosterone and the stress response in juvenile Western Screech-owls: effects of captivity, gender, and activity period. Physiological Zoology. 70. [In press].

Greenwood, P.J. 1980. Mating systems, philopatry, and dispersal in birds and mammals. Animal Behaviour. 28: 1140-1162.

Holberton, R.L.; Parrish, J.D.; Wingfield, J.C. 1996. Modulation of the adrenocortical stress response in neotropical migrants during autumn migration. Auk. 113: 558-564.

Holekamp, K.E. 1986. Proximal causes of natal dispersal in Belding's ground squirrels (*Spermophilus beldingi*). Ecological Monographs. 56: 365-391.

Holekamp, K.E.; Smale, L.; Simpson, H.B.; Holekamp, N.A. 1984. Hormonal influences on natal dispersal in free-living Belding's ground squirrels (*Spermophilus beldingi*). Hormones and Behavior. 18: 465-483.

Howard, W.E. 1960. Innate and environmental dispersal of individual vertebrates. American Midland Naturalist. 63: 152-161.

Jain, M.R.; Patil, P.P.; Subhedar, N. 1993. Direct action of metyrapone on brain: implication in feeding. Neuroreport. 5: 69-71.

Kenward, R.E.; Marcström, V.; Karlbom, M. 1993. Post-nestling behaviour in Goshawks, *Accipiter gentilis*: I. The causes of dispersal. Animal Behaviour. 46: 365-370.

Morton, M.L. 1992. Effects of sex and birth date on premigration biology, migration schedules, return rates and natal dispersal in the Mountain White-crowned Sparrow. Condor. 94: 117-133.

Nilsson, J.-A. 1990. Family flock break-up: spontaneous dispersal or parental aggression? Animal Behaviour. 40: 1001-1003.

Ritchison, G.; Belthoff, J.R.; Sparks, E.J. 1992. Dispersal restlessness: evidence for innate dispersal by juvenile Eastern Screech-owls? Animal Behaviour. 43: 57-65.

Sparks, E.J.; Belthoff, J.R.; Ritchison, G. 1994. Habitat use by Eastern Screech-owls in central Kentucky. Journal of Field Ornithology. 65: 83-95.

Wiggett, D.R.; Boag, D.A. 1993. The proximate causes of male-biased natal emigration in Columbian ground squirrels. Canadian Journal of Zoology. 71: 204-218.

Zulkifli, I.; Dunnington, E.A.; Gross, W.B.; Siegel, P.B. 1993. Inhibition of adrenal steroidogenesis, food restriction and acclimation of high ambient temperatures in chickens. British Poultry Science. 35: 417-426.

Food Habits of the Northern Spotted Owl (*Strix occidentalis caurina*) at Six Nest Sites in Washington's East Cascades

Kenneth R. Bevis[1], Jo Ellen Richards[2], Gina M. King[1], and Eric E. Hanson[1]

Abstract.—This paper reports on 245 pellet samples containing 479 identified prey items collected at six Northern Spotted Owl (*Strix occidentalis caurina*) breeding sites in the eastern portion of its range. The majority of prey (biomass) came from four species; northern flying squirrels (*Glaucomys sabrinus*), bushy-tailed woodrats (*Neotoma cinerea*), northern pocket gopher (*Thomomys talpoides*), and pika (*Ochotona princeps*). Flying squirrels were the most important dietary item, similar to the food habits of spotted owls in more mesic forests of Oregon and Washington.

The Northern Spotted Owl (*Strix occidentalis caurina*) is a medium-sized owl weighing 650-800 g, that inhabits low to mid-elevational mature conifer forests in the Pacific Northwest of the United States. On the east flanks of the Cascade Range, precipitation adequate to support closed canopy forest determines the eastern extent of its range.

This owl has been the subject of intense scientific scrutiny, especially since being designated "threatened" under the Endangered Species Act in 1990. Current research indicates a habitat preference for old-growth and mature forests across its range (Forsman *et al.* 1984, King 1993, Pidgeon 1995, Thomas *et al.* 1990). One of the significant ecological bases for this selection is thought to involve prey availability.

Previous published reports of spotted owl diet focused primarily on habitats in the western, more mesic portions of the species' range (Barrows 1985, Cutler and Hays 1991, Forsman *et al.* 1984). This paper presents results from an analysis of pellets from two study sites east of the Cascade's crest, in drier habitats closer to the margin of the species range.

METHODS

Owls regurgitate the undigested portions of their food in the form of pellets; balls of hair and bones which can be recovered from the ground under roosts or nest sites. These can be broken apart and prey species identified, thus yielding useful information about their food habits.

Pellets, prey remains, and bones remaining after pellets had disintegrated, were collected around nest trees and from the immediate vicinity of known spotted owl nest sites. Items were placed in plastic bags and labeled (site, date collected and number of pellets in each sample). Visual observations of prey items captured or being held by individual owls, were recorded.

Pellets were gathered in 1986 from four nesting sites in the Swauk Creek drainage, approximately 20 km northeast of Cle Elum, Washington. Pellets and prey observations were collected on the Yakama Indian Reservation (YIR) in south-central Washington from 1992-1996 (fig. 1). Diet from two sites on the YIR are analyzed in this paper, with data from six other sites included in the overall totals for the YIR.

Habitats used by spotted owls were similar on both study areas. Nest stands were in mid-elevation (1,000-1,370 m) Grand fir (*Abies grandis*) stands (Franklin and Dyrness 1973).

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[2] U.S. Forest Service, Cle Elum Ranger District, 803 W. 2nd St., Cle Elum, WA 98922.

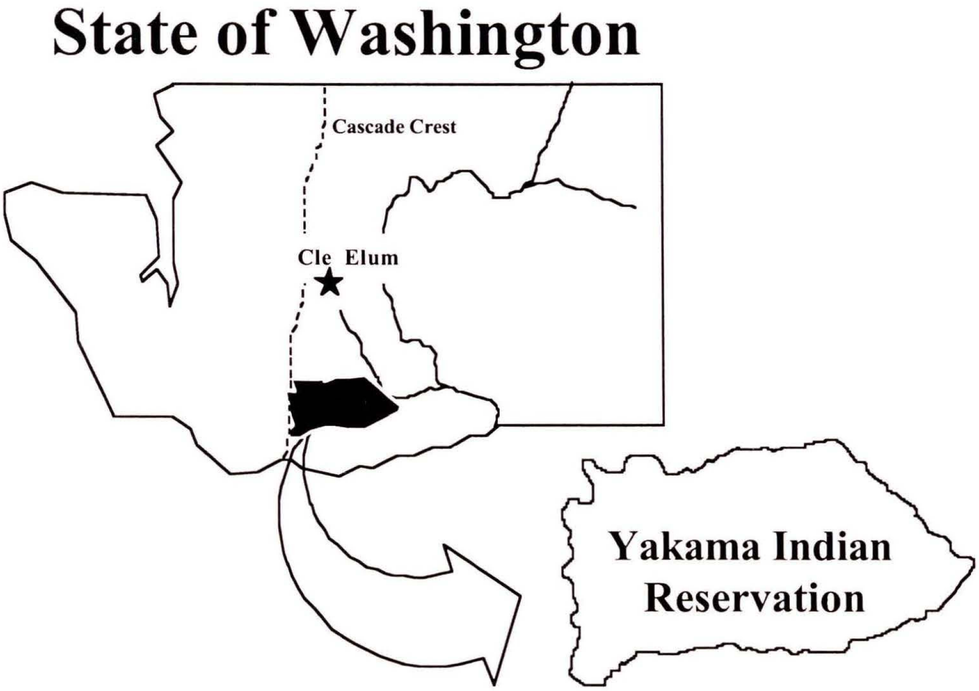

Figure 1.—*Washington State with location of Cascade crest (approximate) and study areas.*

Pellet samples collected from both study areas were treated similarly. Each pellet was placed in a secure numbered fabric bag and soaked in hot soapy water for 24 hours. The Cle Elum pellet bags were machine-washed, rinsed and dried (after large bones were removed), while processing of the YIR pellets was by hand. Identifiable bone and insect pieces were separated using dental tools and tweezers. The hair remains were discarded from the YIR pellets. Microscopic hair analyses were conducted on 27 Cle Elum pellets, with samples mounted on slides using a toluene-based fixative.

Teeth and bones were identified to the lowest possible taxon, usually species, sometimes genus, or at a minimum, to large (>10 0g) or small (<100 g) prey item (Barrows 1985). Skulls and jaws were most diagnostic, though not always present. A key was devised to identify skulls and teeth, based on species expected or known to occur in the study area (Burt and Grossenheider 1980, Hall and Kelson 1959, Hanson 1978, Ingles 1965, Maser and Storm 1970). Richards performed the Cle Elum analyses in 1986 at Colorado State University, Ft. Collins, with the assistance of the Compo-sition Analysis Laboratory and reference skeletons. The YIR specimens were analyzed in the summer and fall of 1996 by four observers using keys and reference skeletons. Identifica-tion of remains in YIR pellets were verified by L. James and S. Rigden.

For each sample, the minimum number of prey items was determined from a count of like skeletal pieces for each species represented. Mean prey weights used to calculate biomass were adopted from existing literature (Burt and Grossenheider 1980, Forsman *et al.* 1984), or calculated from local data. In the case of flying squirrels, average weight was calculated from weights of animals live-trapped on the YIR in 1996. Weights used for large and small prey item analysis were a weighted average of all identified prey. Weights used for biomass calculations for birds were a similar weighted average of identified bird prey items. Insects were identified as prey items, but were not included in calculations due to inability to count individuals, and their estimated small contribution to total biomass consumed.

Diet data were summarized by site, with relative frequency and biomass of prey species calculated for each of the six nest sites. Finally, calculations were repeated with sites pooled by study area.

RESULTS AND DISCUSSION

An analysis of 245 samples yielded 479 individual prey items in 20 vertebrate species (table 1). This list indicates that a wide variety of prey items is eaten by spotted owls in the study areas. Relative frequency (table 2) was used to describe the general make up of the observed prey items by study area.

Table 1. —*Northern spotted owl prey species identified from six nest sites in eastern Washington.*

Size category	Common name	Species
Major large (≥100g) prey species	Northern flying squirrel	*Glaucomys sabrinus*
	Northern pocket gopher	*Thomomys talpoides*
	Bushy-tailed woodrat	*Neotoma cinerea*
	Pika	*Ochotona princeps*
Minor large (≥100g) prey species	Douglas squirrel	*Tamiasciurus douglasii*
	Snowshoe hare	*Lepus americana*
	Townsend mole	*Scapanus townsendii*
Major small (<100g) prey species	Red-backed vole	*Clethrionomys gapperii*
	Deer mouse	*Peromyscus maniculatus*
	Long-tailed vole	*Microtus longicaudus.*
Minor small (<100g) prey species	Mountain phenocomys	*Phenocomys intermedius*
	Townsend's chipmunk	*Tamias townsendii*
	Yellow-pine chipmunk	*Tamias amoenus*
	Pacific mole	*Scapanus orarius*
	Shrew	*Sorex* spp.
	Western tanager	*Piranga ludoviciana*
	Evening grosbeak	*Coccothraustes vespertinus*
	Dark-eyed junco	*Junco hyemalis*
	Red-breasted nuthatch	*Sitta canadensis*
	Hermit thrush	*Catharus guttatus*
	Large beetles/crickets	

Table 2.—*Relative frequencies of prey species by study area.*

Species	Cle Elum (n=352)	YIR (n=113)
G. sabrinus	0.35	0.55
T. talpoides	.08	.05
N. cinerea	.08	.03
O. princeps	.07	.02
Other large	.07	.05
P. maniculatus	.07	.04
C. gapperii	.04	.10
Microtus spp.	.04	.01
Other small	.14	.10
Birds	.06	.06

Table 2 shows an overall similarity in diet on the two study areas. Subtle differences, however, could offer insight into dietary variation across eastern Washington. Flying squirrels were the largest item by proportion on both study areas, with a higher relative frequency on the YIR. Pocket gopher, bushy-tailed woodrat, pika, and other large prey items made up a greater share of the diet on the Cle Elum. More deer mice were taken on Cle Elum, but more red-backed voles were identified on the YIR.

Biomass is considered the best method for comparing dietary information, because it provides a better indication of importance of prey items in meeting individuals' caloric needs. Table 3 summarizes the weights used in this analysis for obtaining biomass estimates.

Table 3.—*Weights used for biomass calculations.*

Species	Weight *grams*	Source
G. sabrinus	140	YIR 1996
N. cinerea	265	Forsman *et al.* 1984
T. talpoides	100	Burt and Grossenheider 1990
O. princeps	158	Forsman *et al.* 1984
Other large	150	Weighted avg.
P. manicula	22	Forsman *et al.* 1984
C. gapperii	29	Maser and Storm 1970
Microtus spp.	54	Maser and Storm 1970 (*M. longicaudus*)
Other small	31	Weighted avg.
Birds, Yakama	43	Avg. of known bird kills on YIR
Birds, Cle E.	21	Richards 1989

On all six breeding sites, large prey comprised the majority of biomass consumed (table 4). Over each study area, large prey items made up 90.5 percent of the biomass on the Cle Elum study area and 91.1 on the YIR (table 5). This indicates that although spotted owls are foraging on small prey items, larger prey are most important for meeting their dietary needs.

These results are similar to other spotted owl diets reported from the Pacific Northwest, with flying squirrels indicated as the dominant food item (Allen and Bicknell 1985, Forsman *et al.* 1984, Thomas *et al.* 1990, Cutler and Hays 1991). The presence in the diet of other large prey items, particularly pocket gopher and pika, suggest varying degrees of opportunistic hunting. For example, on Cle Elum's Green site, a large proportion of the owls' diet was composed of pika. This is probably a reflection of availability of large areas of talus in this area. The high proportion of pocket gopher at Green, and at Vessey on the YIR, may indicate foraging in open forests or meadows where gophers occur (Ingles 1965). These sites contrast to owl sites such as Howard on the YIR, with an extensive closed canopy forest setting, where flying squirrels are the dominant prey item.

This analysis suggests that selection for flying squirrels is taking place. Northern Spotted Owls prefer mature forest habitats, perhaps because flying squirrels reach their greatest densities in these habitats (Carey 1991).

MANAGEMENT AND RESEARCH RECOMMENDATIONS

Protecting habitat for prey species is undoubtedly an important element of spotted owl conservation, especially in landscapes subject to logging. Further work is needed on the habitat needs of these species, particularly the flying squirrel. This work should focus on stand structure attributes needed by these prey species, such as snags, logs, and dwarf mistletoe. With a greater understanding of owl prey ecology, we might better provide for the needs of the Northern Spotted Owl into the future.

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Table 4.—*Prey species as percent biomass of diet at six Northern Spotted Owl nest sites on the east slope of the Washington Cascades.*

Species	Cle Elum				YIR	
	Swauk (n^1=139)	Liberty (n^1=66)	Hovey (n^1=109)	Green (n^1=38)	Howard (n^1=50)	Vessey (n^1=45)
Glaucomys sabrinus	59	37	41	28	68	65
Thomomys talpoides	9	7	4	13	2	12
Neotoma cinerea	12	23	25	12	4	6
Ochotona princeps	5	10	9	35	5	0
Other Large[2]	3	16	11	7	15	0
Combined Small[3]	13	7	9	6	6	15

[1] Total number of prey items identified from each site.
[2] Includes *Lepus americana* and unidentified bones of prey items >100 g.
[3] All prey species <100 g.

Table 5.—*Prey species as percent biomass of Northern Spotted Owl diet by study area on the east slope of the Washington Cascades.*

Species	Cle Elum (n^1=352)	YIR (n^1=95)
Glaucomys sabrinus	45	70
Thomomys talpoides	8	5
Neotoma cinerea	19	6
Ochotona princeps	11	3
Other large[2]	9	7
Combined small[3]	9	9

[1] Total number of prey items identified on all sites within study area.
[2] Includes *Lepus americana* and unidentified bones of prey items >100 g.
[3] All prey species <100 g.

LITERATURE CITED

Barrows, C.W. 1985. Breeding success relative to fluctuations in diet for Spotted Owls in California. Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station: 50-54.

Burt, W.H.; Grossenheider, R.P. 1980. A field guide to the mammals. New York, NY: Houghton-Mifflin Co. 287 p.

Carey, A.B. 1991. The biology of arboreal rodents in Douglas-fir forests. Gen. Tech. Rep. PNW-276. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 46 p.

Cutler, T.L.; Hays, D.W. 1991. Food habits of Northern Spotted Owls in high elevation forests of Pelican Butte, southwestern Oregon. Northwestern Naturalist. 72: 66-69.

Forsman, E.D.; Meslow, E.C.; Wight, H.M. 1984. Distribution and biology of the Spotted Owl in Oregon. Wildlife Monographs. 87: 64 p.

Franklin J.T.; Dyrness, C.T. 1973. Natural vegetation of Oregon and Washington. Gen. Tech. Rep. PNW-8. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 332 p.

Hall, E.R.; Kelson, K.R. 1959. The mammals of North America. Vol. I. New York, NY: Ronald Press. 1,089 p.

Hanson, E.E. 1978. The impact of a prescribed burn in a temperate subalpine forest upon the breeding bird and small mammal populations. Ellensburg, WA: Central Washington University. 56 p. M.S. thesis.

Ingles, L.G. 1965. Mammals of the pacific states. Stanford, CA: Stanford University Press. 506 p.

King, G.M. 1993. Habitat characteristics of Northern Spotted Owls in eastern Washington. Berkeley, CA: University of California, Berkeley. 77 p. M.S. thesis.

Maser, C.; Storm, R.H. 1970. A key to the microtinidae of the pacific northwest (Oregon, Washington, Idaho). Corvallis, OR: Oregon State University Bookstore. 162 p.

Pidgeon, A.M. 1995. Habitat characteristics of Northern Spotted Owls in the unmanaged forest of the Yakama Indian Reservation, eastern Washington. Ellensburg, WA: Central Washington University. 87 p. M.S. thesis.

Richards, J.E. 1989. Spotted Owl food habits and prey availability on the east slope of the Washington Cascades. Ft. Collins, CO: Colorado State University. 45 p. M.S. thesis.

Thomas, J.W.; Forsman, E.D.; Lint, J.B.; Meslow, E.C.; Noon, B.R.; Verner, J. 1990. A conservation strategy for the Northern Spotted Owl. Portland OR: U.S. Department of Agriculture, Forest Service, and U.S. Department of Interior, Bureau of Land Management, Fish and Wildlife Service, and National Park Service. 427 p.

Autumn Migration of Northern Saw-whet Owls (*Aegolius acadicus*) in the Middle Atlantic and Northeastern United States: What Observations from 1995 Suggest

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Abstract.—During the autumn of 1995 more than 5,900 migrant Northern Saw-whet Owls were banded in eastern and central North America. Though typical numbers of owls were banded at most Great Lakes stations during 1995, a record number were netted at Hawk Ridge, near Duluth, Minnesota and, when compared with more normal years, a remarkably disproportionate 40 percent of the total were banded at 5 stations in New Jersey, Maryland, and Virginia. The movement occurred throughout the eastern U.S. and may have been comparable to that of 1965 when unusually high numbers of Northern Saw-whet Owls were netted at songbird banding stations throughout the northeastern U.S. In the Mid-Atlantic states, the 1995 movement was comprised largely of immature females, with the proportion of males decreasing as latitude decreased. Many owls migrating through the Mid-Atlantic states probably wintered south of Virginia. None of our banded owls were recovered as northbound spring migrants along the southern shores of the Great Lakes. Interstation retraps and other autumn recoveries present a pattern that suggests that the forests of the southeastern United States may be an important wintering area for a portion of the eastern continental population of Northern Saw-whet Owls.

Each autumn many Northern Saw-whet Owls (*Aegolius acadicus*) leave their breeding range at northern latitudes and migrate to wintering areas (Holroyd and Woods 1975, Weir *et al.* 1980). This movement has been well documented by banding at stations in the Great Lakes area (Mueller and Berger 1967, Weir *et al.* 1980, Erdman *et al.* 1997, Evans 1997). Movement of Northern Saw-whet Owls along the Atlantic coast and in the Northeast has received much less attention, with only Cape May in operation from 1973 to 1990 (Duffy and Kerlinger 1992).

Beginning in 1991, additional stations began operations in the Mid-Atlantic and each had captured < 200 Northern Saw-whet Owls each autumn. During 1995, the Mid-Atlantic stations witnessed a surprisingly large movement of owls: 2,596 Northern Saw-whet Owls were captured at five stations in New Jersey, Maryland, and Virginia. Analysis of the owls captured in 1995 revealed details on the origin of the flight, the speed of movement between stations, and the age and sex composition of migrants. From these data we will suggest what we can about the characteristics of this unusually large movement of Northern Saw-whet Owls during the autumn of 1995.

STUDY AREAS AND METHODS

Coastal Banding Stations

Cape May Point, NJ

(38°50' N, 74°50' W, elevation 1 m, see figure 1). Eleven single height mist nets were operated at a site in South Cape May Meadows, a Nature

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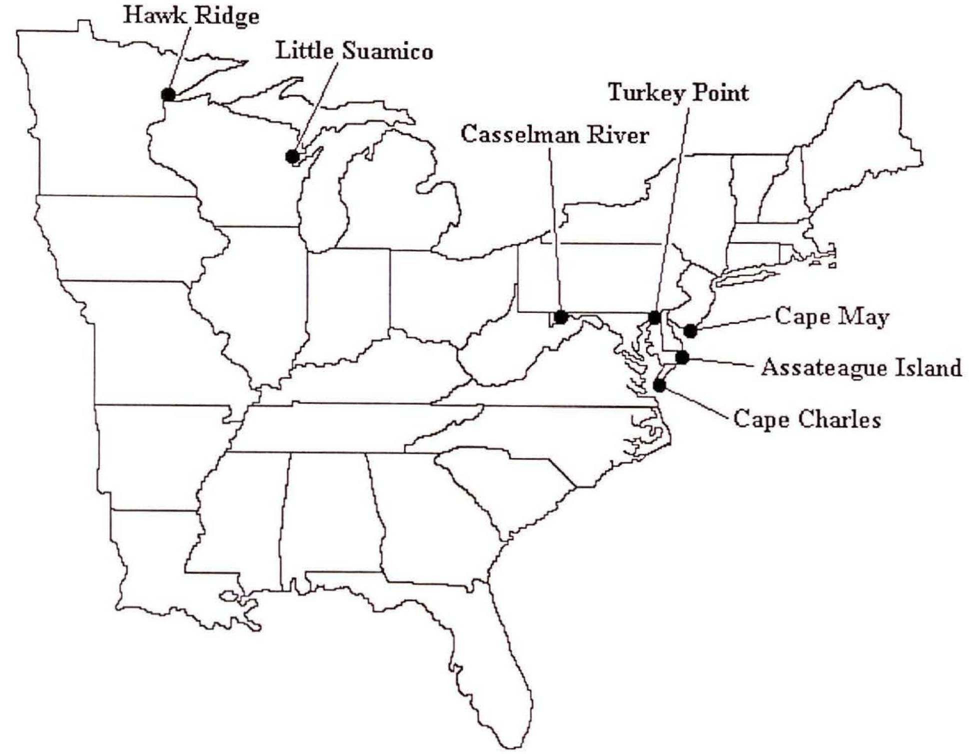

Figure 1.—*Location of banding stations mentioned in the text where autumn migrant Northern Saw-whet Owls were banded during the 1991-1996 period.*

Conservancy preserve, approximately 75 m behind the primary dune for 19 nights from October 24 through November 19, 1995. Surrounding habitats consisted of a wet meadow of marsh elder (*Iva frutescens*), groundsel bush (*Baccharis halimi-folia*), scattered red cedar (*Juniperus virginiana*) and a woodlot of mixed deciduous trees with a dense understory of poison ivy (*Toxicodendron radicans*). Ten additional single height nets were located 150 m north between a dense stand of red cedar and a salt marsh. A second station in the Higbee Beach Wildlife Management Area, 3 km north, consisted of eight single height mist nets and was operated on 7 nights from November 4-18. Nets were placed in a cultivated field of mixed forbs adjacent to a hedgerow thicket of Japanese honeysuckle (*Lonicera japonica*), multiflora rose (*Rosa multiflora*) and Virginia creeper (*Parthen-ocissus quinquefolia*).

Assateague Island, MD

(38°10' N, 75°10' W, elevation 2 m, see figure 1) Seven mist nets were operated within a loblolly pine (*Pinus taeda*) forest on an old dune system approximately 650 m west of the Atlantic Ocean shoreline in Assateague Island National Seashore. Mist nets were arranged as a line of six nets with a seventh perpendicular net on the north side of the line at its mid point. The four central nets of the line and the perpendicular net were two nets high and the two outermost nets of the line were one net high. The station was operated nightly from October 22 through December 2, 1995.

Cape Charles, VA

In a 10-km^2 area at the southern tip of the Delmarva Peninsula near Cape Charles (fig. 1), three net locations were operated nightly from October 21 through December 13, 1995. At each site a line of six single height mist nets was used. One set of nets was located in the Eastern Shore of Virginia National Wildlife Refuge near the southern tip of the Delmarva Peninsula (37°00' N, 75°50' W, elevation 1 m). Nets at this site were approximately 50-100 m from beaches on the bayside to the west, salt marsh to the east, and the mouth of the Chesapeake Bay to the south. The vegetation consisted of loblolly pine forest with a dense understory of wax myrtle (*Myrica pennsylvanicus*). The second net site was in the Gatr Tract/Mockhorn Island Wildlife Management Area along the oceanside of the peninsula approximately 3 km north of the first site (37°10' N, 75°50' W, eleva-tion 2 m). Nets were approximately 100 m west of the salt marsh in a loblolly pine forest with a moderate understory of various woody shrubs. The last set of nets was located in Kiptopeke State Park on the bay side of the peninsula approximately 3 km north of the first site (37°00', 75°50' W, elevation 10 m). The nets were approximately 100 m east of the beach in a forest dominated by oaks (*Quercus* sp.) with scattered loblolly pines and a sparse understory of American holly (*Ilex opaca*).

Inland Banding Stations

Turkey Point, MD

(39°20' N, 76°00' W, elevation 24 m, see figure 1) This station was located in Elk Neck State Park near the tip of the Elk Neck Peninsula at the upper end of the Chesapeake Bay. Four mist nets, two nets high, were placed in a roughly straight line at the edge of a small clearing in second-growth deciduous forest approximately 500 m north of the tip of the point. This site was operated on most nights from October 22 through November 25, 1995.

Casselman River, MD

(39°30' N, 79°10' N, elevation 780 m, see figure 1) The banding station was located on the Appalachian Plateau in a broad shallow valley along the upper reaches of the North Branch of the Casselman River 40 km southwest of Cumberland, MD. Seven mist nets, two nets high, were arranged in a relatively straight line through a small clearing in an eastern hemlock (*Tsuga canadensis*) forest. Nets were operated nightly from October 7 through November 26, 1995.

Net Operation and Banding

All stations used audiolures (Erdman and Brinker 1997) that produced sound pressure levels of 100-110 dB at 2 m and identical tapes to enhance capture rates. Mist nets at all stations were generally 12 m long, 2 m high, 61 mm mesh; some larger and smaller mesh sizes were used at Cape May and Cape Charles. Nets were opened at dusk, checked every 1-2 hours and closed about dawn. At all stations except Cape May, nets were opened on every night with acceptable weather between the opening and closing dates given above. Nets were not operated during precipitation or on extremely windy nights. Captured owls were fitted with U.S. Fish and Wildlife Service leg bands, weighed, measured, and aged. Owls with one generation of wing feathers were classified as immatures (HY=hatch year); owls with more than one age of wing feathers were aged as adults (AHY=after hatch year) (Evans and Rosenfield 1987). The pattern of retained old feathers was recorded for most adults.

Sex Determination

Weir *et al.* (1980) first published criteria for determination of sex in Northern Saw-whet Owls from wing chord measurement; other authors have commented that the criteria were flawed because observed sex ratios differed from 1:1 (Mueller 1982, Evans and Rosenfield 1987, Slack 1992). The wing chord method of determining sex for Northern Saw-whet Owls does not work reliably and for this analysis it was not used to assign sex to individual owls. A discriminant function (DF) was developed that relied upon a combination of wing chord and mass to assign sex to owls (see Appendix). The DF assigned sex to more than 90 percent of the owls. Solely for the purpose of this analysis, the DF was considered adequate and much more reliable than using wing chord to determine sex.

RESULTS

During the autumn of 1995, five owl banding stations in New Jersey, Maryland, and Virginia netted 2,596 Northern Saw-whet Owls (table 1). The Turkey Point, MD station, which was only operated during 1995, netted 324 Northern Saw-whet Owls. The five-station total represented more than 40 percent of the Northern Saw-whet Owls banded in the Eastern U.S. during the autumn migration of 1995. During more usual years the total number of owls banded in this portion of the U.S. is at most several hundred. Correcting for effort, the capture rate (owls/10 m^2 net/100 hours) during the years 1991-1994, varied from a low of 0.211 at Assateague during 1992 to a high of 2.83 at Cape May during 1993. In comparison, capture rates during 1995 varied from 2.00 to 6.61 (table 1). Although more comparable than total number of owls netted, catch per unit effort values are still not directly comparable, primarily because of differences in the timing and duration of capture efforts between stations each year.

During 1995 there were 31 direct interstation recoveries between the banding stations at Cape May, Assateague, and Cape Charles (fig. 2). Five owls banded at Cape May were subsequently retrapped at Assateague. Fifteen owls

Table 1.—*Northern Saw-whet Owls captured with an audiolure and mist nets, nights of netting effort, and adjusted capture rates at four Mid-Atlantic banding stations from 1991-1996.*

Station		**Year**					
		1991	**1992**	**1993**	**1994**	**1995**	**1996**
Cape May, NJ	owls netted	82	24	187	73	637	-[1]
	nights open	23	17	28	23	20	-
	owls/ 10 m² net/ 100 hours	1.48	0.70	2.83	1.00	6.61	-
Assateague Island, MD	owls netted	65	29	63	27	332	21
	nights open	32	43	29	33	38	36
	owls/ 10 m² net/ 100 hours	0.486	0.211	0.614	0.220	2.59	0.168
Casselman River, MD	owls netted	-[1]	44	148	89	296	63
	nights open	-	38	45	44	38	55
	owls/ 10 m² net/ 100 hours	-	0.375	0.802	0.459	2.00	0.287
Cape Charles, VA	owls netted	-[1]	-	-	52	1,007	106
	nights open	-	-	-	32	44	42
	owls/ 10 m² net/ 100 hours	-	-	-	0.314	4.43	0.502

[1] The banding effort at Cape May during the autumn of 1996 was significantly different than during previous years and is not comparable with effort during the 1991-1995 period. At other stations the - represent years for which no data is available.

banded at Cape May were later retrapped at Cape Charles. An additional 11 owls banded at Assateague were retrapped at Cape Charles. Two of the owls banded at Turkey Pt. were retrapped at other banding stations as direct recoveries. One owl went to Cape Charles (banded November 5, 1995, recaptured November 18, 1995) and the other was renetted at an owl banding station near Halifax, North Carolina (36°10' N, 77°30' W) on November 25, 1995 (banded October 30, 1995). One Saw-whet Owl from Cape May, banded on November 16, 1995, was also renetted at Halifax, NC, on December 3, 1995. Finally, one owl banded at Assateague on November 12, 1995 was recaptured on the campus of the College of William & Mary (37°10' N, 76°40' W) on February 14, 1996. No owls banded at the Casselman River station were retrapped or recovered during the autumn-winter of 1995-96 (fig. 2). None of the owls banded at our five stations during the autumn of 1995 were retrapped as northbound migrants at stations along the southern shores of the Great Lakes during the spring of 1996.

Several owls banded outside the region were renetted or recovered in the Mid-Atlantic region during autumn 1995 (fig. 2). Two owls banded on October 26 and 27, 1994 near Wells, ME (43°10' N, 70°30' W), were renetted within a few nights of each other, on November 13, 1995 at Cape May, NJ and on November 16, 1995 at Turkey Pt., MD. A Northern Saw-whet Owl banded at Little Suamico, WI, (44°40' N, 87°50' W), on September 29, 1995 was renetted at Halifax, NC on November 8, 1995 (T. Erdman, pers. comm.). This owl represents the first direct recovery of a autumn migrant Northern Saw-whet Owl from the Great Lakes region that crossed the Appalachian Mountains. Another owl, banded at Hawk Ridge, MN (46°50' N,

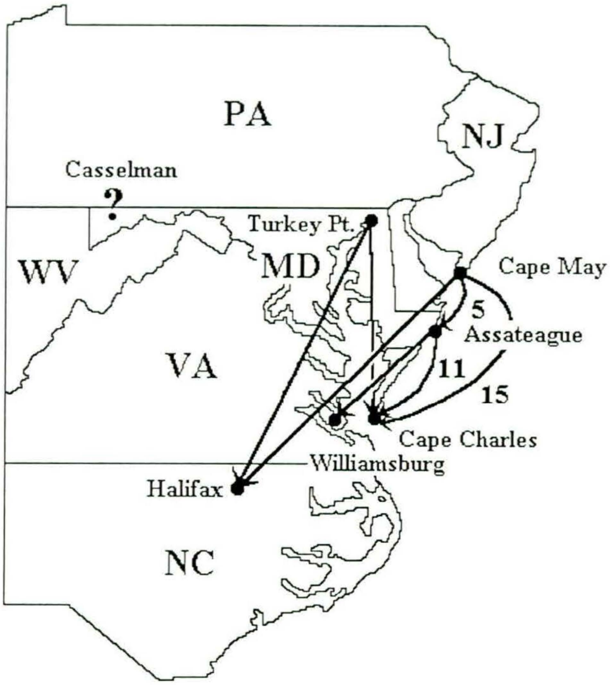

Figure 2.—*Between banding station movements of Northern Saw-whet Owls in the Mid-Atlantic states during the autumn of 1995. No owls were retrapped moving north, and no owls from Casselman River were retrapped.*

92°00' W) during the autumn of 1995 was recovered near East New Market, MD (38°30' N, 75°50' W) during March 1996 (D. Evans, pers. comm.).

During 1995 Northern Saw-whet Owls moved rapidly into and/or through the Mid-Atlantic region (table 2). One immature, released at Cape May near dawn (05:15) on November 17, was recaptured at Assateague Island, 88 km south, 3 hours after darkness (21:00) on the same day, for a minimum speed of nearly 30 km/h of darkness. Traveling from Cape May directly south to Assateague involves a 19 km crossing of Delaware Bay; obviously forced to make this crossing non-stop, this over water flight required less than 40 minutes. When released at Cape May, this owl's mass was 100 g; when recaptured at Assateague it weighed 99 g. Three other owls traveled from Cape May to Assateague within 3 nights. These three owls traveled an average of 29 km per night, nearly as fast as the owl that went from Little Suamico to Halifax, NC (average nightly movement, 32 km). The two interstation recaptures of owls banded at Turkey Point traveled an average distance of 13 and 18 km per night.

While two Northern Saw-whet Owls journeyed from Cape May to Cape Charles within 4 nights (average nightly movement, 56 km), eight other individuals took from 6 to 15 nights and six owls took more than 20 nights (27-65 nights) to make the trip. The shortest recapture interval between Cape May and Cape Charles yielded a minimum speed of 5.6 km/h of darkness. The Cape May owl recaptured in North Carolina traveled an average distance of 20 km per night. Data from owls banded at Assateague and retrapped at Cape Charles are similar (table 2). The shortest interstation interval between Assateague and Cape Charles yielded a minimum speed of 3.1 km/h of darkness. As the distance between stations increased the estimated average rate of migration decreased (table 2).

The autumn 1995 Northern Saw-whet Owl movement was characterized by a high proportion of immature owls (table 3). During the 1991-1994 period, the proportion of the owls that were adults varied considerably between stations and years, ranging from 10 to 63 percent. In any given year, age ratios during the 1991-1994 period showed more disparity between stations than in 1995 when all stations netted few adult owls.

Females were the most frequently netted Northern Saw-whet Owls during 1995 (table 3). Overall the DF assigned sex to 91 percent of the 3,263 owls for which both wing chord and mass measurements were taken (table 3). Along the coast, the proportion of the netted owls that were male increased with latitude, from 14 percent at Cape Charles to 18 percent at Cape May. The percent of the netted sample classed as unknown sex also increased with latitude. Females comprised 83 percent of the Northern Saw-whet Owls netted at the Casselman River in 1995 (table 3). At all stations, adult males were the least frequently captured individuals. Adult males were similarly rare during the 1991-1994 period (table 4).

Northern Saw-whet Owls netted during 1995 were in noticeably poorer body condition than those netted during 1991-1994. Many owls carried little or no fat in the furcular depression. This was in marked contrast to other years when furcular fat was frequently

Table 2.—*Nights between initial capture and subsequent recapture for Northern Saw-whet Owls moving between three Mid-Atlantic banding stations during the autumn of 1995. Values are the number of owls that took the indicated number of nights to travel between banding stations.*

Number of nights	Cape May to Assateague Island[1]	Assateague Island to Cape Charles[2]	Cape May to Cape Charles[3]
1	1	0	0
2	1	0	0
3	2	1	1
4	0	1	1
5	0	0	0
6	0	0	1
7	0	2	0
8	0	2	1
9	0	1	0
10	1	0	2
11	0	0	0
12	0	1	1
13	0	3	1
14	0	0	1
15	0	0	1
>15	0	0	6
Mean (nights)	3.8	8.8	16.0[4]
Mean km/night	23.1	15.6	14.1[4]

[1] Cape May to Assateague Island is 88 km.

[2] Assateague to Cape Charles is 137 km.

[3] Cape May to Cape Charles is 225 km.

[4] Two retraps after 15 Dec. were excluded from the mean.

observed (Brinker, Erdman, pers. observ.). Mean body mass by age and sex class is summarized in table 4. At all stations with more than 3 years of data, immature females during 1995 weighed less than those netted at the same stations during any earlier year. Other than the overall low mass of female owls netted during 1995, there was no readily discernible pattern in mean weight variation among years, age classes, or sexes.

DISCUSSION

Origin of the Owls

Data on the origin of Northern Saw-whet Owls migrating through the Mid-Atlantic is limited by the lack of any significant banding effort to the north. We suspect that the bulk of the owls observed in the Mid-Atlantic States during autumn 1995 originated in eastern Canada and the northeastern U.S. This is inferred primarily from observations reported regionally (see Audubon Field Notes). Other support is provided by the two owls from Maine recaptured at Cape May and Turkey Point, by an owl banded on October 24, 1995 at Casselman River that was retrapped on October 17, 1996 in southeastern Maine (39°30' N, 79°10' W), and by two recoveries in southern Ontario during 1996 of owls banded on Assateague Island during the autumn of 1995. Interstation retraps of Northern Saw-whet Owls are much more likely than recovery of dead individuals. Had there been more banding effort in eastern Canada and the northeastern U.S., more inter-station recoveries would have been available for review. Additional support for a northeastern origin comes from the greater magnitude of the flight in the Mid-Atlantic compared to what was observed in Wisconsin and Minnesota (see below). Had most of the owls originated farther

Table 3.—*Northern Saw-whet Owl age and sex composition at four Mid-Atlantic banding stations from 1991-1996. Age and sex values are percent of sample size (n). Only owls of known age with both mass and wing cord measurements were included, therefore, sample sizes may sometimes be less than the total number of owls captured in a given year.*

Station		Year					
		1991	1992	1993	1994	1995	1996
Cape May, NJ	n	81	24	187	72	637	-[1]
	Adults	56	58	10	38	14	-
	Females	81	83	76	86	69	-
	Males	12	17	13	10	18	-
	Unknown	7	0	11	4	13	-
Assateague Island, MD	n	63	29	60	26	324	21
	Adults	29	38	15	20	12	71
	Females	76	90	92	96	72	90
	Males	16	3	8	4	16	10
	Unknown	8	7	0	0	12	0
Casselman River, MD	n	-[1]	43	147	89	296	63
	Adults	-	53	39	45	24	76
	Females	-	93	94	94	83	95
	Males	-	0	1	3	8	3
	Unknown	-	7	5	3	9	2
Cape Charles, VA	n	-[1]	-	-	52	980	102
	Adults	-	-	-	63	17	86
	Females	-	-	-	85	75	87
	Males	-	-	-	12	14	6
	Unknown	-	-	-	4	11	7

[1] The banding effort at Cape May during the autumn of 1996 was significantly different than during previous years and age/sex class data was not considered comparable with that from the 1991-1995 period. At other stations the - represent years for which no data is available.

west, greater numbers of owls should have been netted in the western Great Lakes. However, an unknown proportion of the Northern Saw-whet Owls that were found in the Mid-Atlantic and southeastern states during 1995 did come from the western Great Lakes. This is in contrast to more normal years when owls from the western Great Lakes are thought to be much less frequent. The two owls that reached Maryland and North Carolina from Hawk Ridge and Little Suamico were the first direct recoveries of western Great Lakes banded Northern Saw-whet Owls east of the Appalachian Mountains. All previous Midwest to Mid-Atlantic recoveries have been indirect (at least one breeding season intervened between the original banding and the subsequent recapture) and were in the Appalachian Mountains, not the Coastal Plain.

Magnitude of the Movement

The number of Northern Saw-whet Owls in the Mid-Atlantic states during the autumn of 1995 was exceptional. Capture rates during 1995 were several times greater than in previous years (table 1). The increase in the East was much larger than in the western Great Lakes (fig. 3), where Hawk Ridge exceeded its highest previous season by only 27 percent. At Little Suamico, 28 percent fewer owls were banded during 1995 than in the previous high season in 1988 and the numbers in both 1993 and 1994 were slightly higher than in 1995.

It is difficult to compare the size of the 1995 Mid-Atlantic Northern Saw-whet Owl movement with flights prior to 1989, the year when an audiolure was first used at Cape May.

Table 4.—*Mean mass by age and sex class of Northern Saw-whet Owls captured at four Mid-Atlantic banding stations from 1991-1996. Values are in grams and sample sizes are in ( ). Only owls of known age with both mass and wing cord measurements were included, therefore, sample sizes may sometimes be less than the total number of owls captured in a given year.*

Station		**Year**					
		1991	**1992**	**1993**	**1994**	**1995**	**1996**
Cape May, NJ	Adult Female	94.0	94.7	94.1	96.9	93.7	-[1]
	(n)	(44)	(11)	(14)	(23)	(63)	
	Adult Male	81	77.0	75	79.0	77.3	-
	(n)	(1)	(3)	(1)	(3)	(3)	
	Immature Female	94.3	94.9	94.9	96.5	93.8	-
	(n)	(22)	(9)	(128)	(39)	(326)	
	Immature Male	76.1	78	79.1	80.5	77.7	-
	(n)	(8)	(1)	(23)	(4)	(139)	
Assateague Island, MD	Adult Female	97.1	95.4	96.7	91.2	94.7	95.5
	(n)	(16)	(10)	(9)	(6)	(26)	(14)
	Adult Male	79	70	-[1]	-	80.5	78
	(n)	(1)	(1)			(6)	(1)
	Immature Female	97.5	95.9	97.3	95.9	94.3	94.0
	(n)	(32)	(16)	(46)	(18)	(207)	(5)
	Immature Male	78.9	-	78.0	80	78.4	74
	(n)	(9)		(5)	(1)	(47)	(1)
Casselman River, MD	Adult Female	-[1]	94.7	95.3	94.6	94.1	96.4
	(n)		(21)	(56)	(38)	(65)	(47)
	Adult Male	-	-	-	81.0	78.5	83
	(n)				(2)	(2)	(1)
	Immature Female	-	97.4	96.6	95.1	94.4	98.1
	(n)		(19)	(82)	(46)	(182)	(13)
	Immature Male	-	-	78.0	82	76.8	78
	(n)			(2)	(1)	(21)	(1)

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[1] The banding effort at Cape May during the autumn of 1996 was significantly different than during previous years and mass data was not considered comparable with that from the 1991-1995 period. At other stations the - represent age/sex classes for which no data is available.

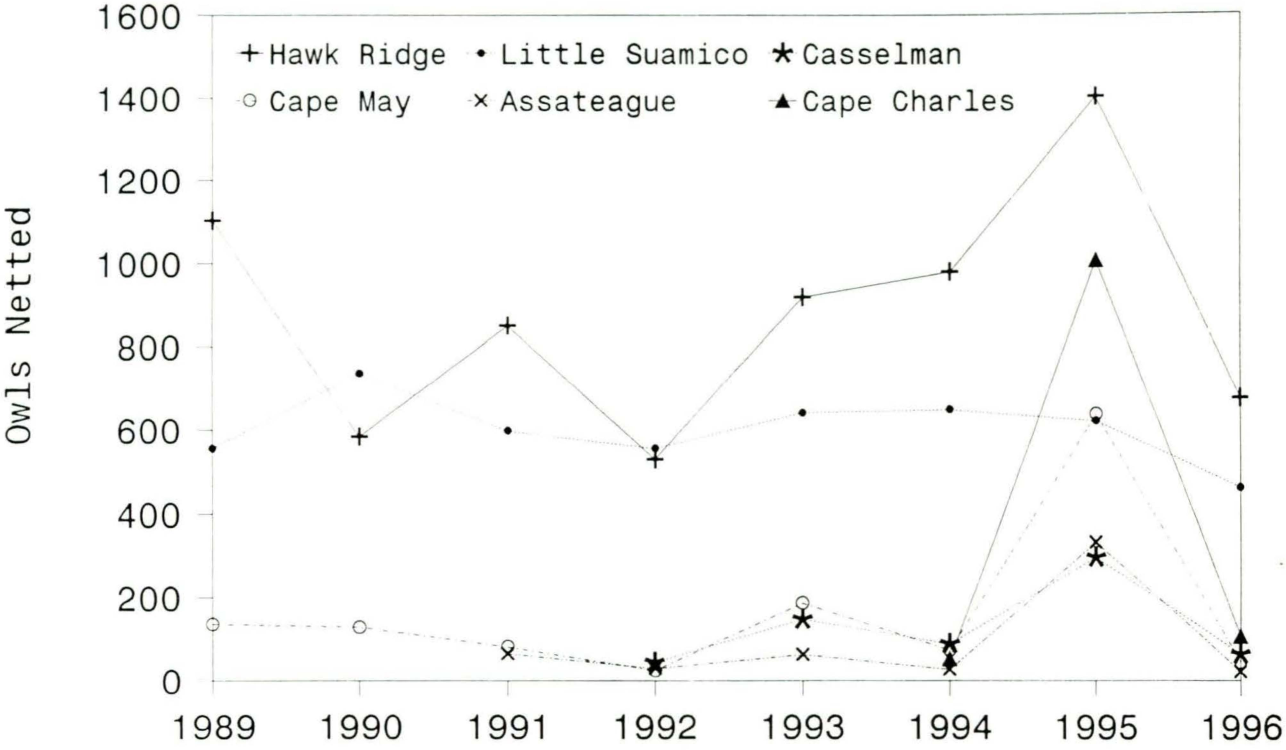

Figure 3.—*Number of Northern Saw-whet Owls captured during autumn migration at two Western Great Lakes and four Mid-Atlantic banding stations from 1989-1996.*

Audiolures increase capture rates from 4 to 10 times (Erdman and Brinker 1997). Without the use of an audiolure, previous high years at Cape May were 1980 and 1981, when 115 and 109 saw-whet owls were netted, respectively (Duffy and Kerlinger 1992). If an audiolure had been used in 1980 and 1981, captures at Cape May may have been comparable to 1995.

The only other year when an exceptionally large migration of Northern Saw-whet Owls was noted in the eastern U.S. occurred in 1965. During the autumn of 1965 large numbers of owls were captured at many songbird banding stations (Davis 1966). For example, on the morning of October 17, 1965, 29 saw-whet owls were passively netted at Kent Point, MD (38°50' N, 76°20' W) (Reese 1966). In an attempt to put the 1965 move-ment into perspective, Bird Banding Laboratory records of Northern Saw-whet Owls banded at all songbird banding stations in Maryland from 1957 through 1985 were reviewed. Banding efforts directed specifically toward migrant Northern Saw-whet Owls were initiated in Maryland during 1986 and data from songbird banding stations after 1985 are overwhelmed by the targeted efforts. The pre-1986 data show that during most years fewer than 10 owls were banded statewide. More than 11 were banded during only 3 years; 1965, 1968, and 1973. Except for 1965, the maximum banded in any one year was 26; during 1965, 65 Northern Saw-whet Owls were banded in Maryland.

The 1995 movement began early, a characteristic that was also observed during 1965 (Davis 1966). For example, the normal autumn migration period in eastern Maryland is October 25-November 15, while during 1965 the passive netting of 29 owls at Kent Point occurred on October 17 (Reese 1966). During 1995 the only station to open early was Casselman River, which opened on October 7. By October 25, 127 Saw-whet owls had been netted, 43 percent of the Casselman's 1995 season total. The other stations opened on their usual schedules and immediately netted significant numbers of owls.

Despite the observations accumulated during 1995, there is no definitive way to compare what we observed during the autumn of 1995 to 1965. Thus, the relative size of the two movements cannot be fairly judged at this point in time.

Age and Sex Composition

Our observations from 1995 suggest that differential migration, as has been reported for the Tengmalm's Owl (*Aegolius funereus*) in Finland (Korpimaki 1987), may be an important part of the life history of this species. The autumn 1995 migration of Northern Saw-whet Owls into and through the Mid-Atlantic States was comprised mostly of immature females (fig. 4). However, during most years immature females are the predominant age-sex class and the only years when immature females do not predominant are low years, when adult females predominate (table 3). During 1995, the next most predominant age-sex class was immature males. The most infrequent age-sex class was adult males. These results are not entirely surprising as years with higher numbers captured are characterized by larger proportions of immature owls (table 3) (Weir *et al.* 1980, Duffy and Kerlinger 1992). The decline in males with latitude that we observed is probably real. In the only other North American owl that differential migration has been reported for, adult female Snowy Owls (*Nyctea scandiaca*) winter the farthest north and immature males the farthest south (Kerlinger and Lein 1986).

Interstation Movements

Recaptures of three banded Northern Saw-whet Owls (one each from Assateague, Cape May, and Turkey Point) provided evidence that movement of at least some individuals continued south of Cape Charles. The latter two of these owls went to North Carolina and the other was retrapped in Williamsburg, VA.

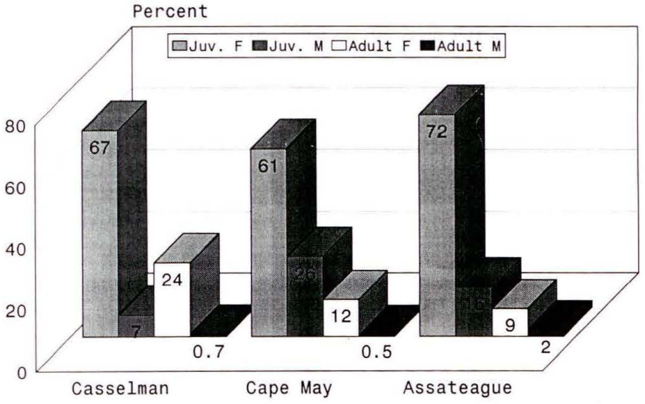

Figure 4.—*Age/sex class composition of autumn migrant Northern Saw-whet Owls at three Mid-Atlantic banding stations during 1995.*

Movement deep into the southeastern U.S. is not unusual. At their farthest known extent south, Northern Saw-whet Owls have been found in northern Florida two times (Lesser and Stickley 1967, Miller and Loftin 1984). Movements south to Florida even occur in years when few Northern Saw-whet Owls migrate into the Mid-Atlantic States. For example, during 1996, when few Northern Saw-whet Owls migrated into the Mid-Atlantic States, a live immature female was found near Pensecola, FL (Woolfenden, pers. comm.).

After reaching Cape May Point, at the southern tip of New Jersey, some owls moved in a northerly direction. Three Northern Saw-whet Owls banded at Cape May were found as road kills less than 8 km north of the banding location 9 (one owl) and 30 (two owls) days after banding, while another was found as a road kill 90 km north of the banding site 38 days after banding. Northward movement may result from a reluctance to cross Delaware Bay or from an abundance of suitable wintering habitat north of Cape May. Four of the five banding stations, particularly the coastal stations, are located in, or in close proximity to, suitable wintering habitat. During 1995 substantial numbers of owls remained in the Mid-Atlantic area for the winter. In a mark-recapture experiment designed to estimate the density of wintering owls on Assateague Island, 56 percent of the 59 individuals netted during January-March 1996 had been banded on Assateague during the autumn of 1995 (Brinker, unpubl. data). There also may have been additional facultative movements of owls during the winter of 1996 in response to unusually severe winter weather with significant snow accumulations along the East Coast. During the mark-recapture experiment waves of unbanded individuals were netted when radio-marked owls disappeared (Brinker and Churchill, unpubl. data).

Lack of interchange between Casselman River and the other four stations suggests that Northern Saw-whet Owls captured at Casselman River may have different origins, migratory paths, and/or wintering areas than those captured at the four Coastal Plain stations. Since banding was initiated in western Maryland during 1986, 901 Northern Saw-whet Owls have been banded and the only retrap or recovery away from western Maryland was the owl retrapped in Maine during the autumn of 1996. In western Maryland, there have been three indirect recoveries of owls previously banded in the western Great Lakes, one each from Hawk Ridge, Little Suamico, and Whitefish Point, MI (46°40' N, 84°50' W).

Theoretical Framework

After 30 years of collective work and over 50,000 owls banded, can a hypothesis be put forth that attempts to unify what we know of Northern Saw-whet Owl migratory movements in eastern North America? Possibly. In this section we attempt to formulate a working hypothesis that can be used to organize and direct future research on Northern Saw-whet Owl migration.

Northern Saw-whet Owls are relatively small, with an average female mass of about 95 g and an average male mass of about 77 g. This species may have difficulty maintaining body condition and/or temperature in the face of food stress during cold or snowy winters, when acquiring prey may be difficult. Korpimaki (1987) summarized life history traits for Tengmalm's Owls that revolve around body size, sexual dimorphism, and ability to capture prey during winter. An important part of Korpimaki's model of Tengmalm's Owl winter ecology involved differential geographic movement, where females were more migratory than males. Male Tengmalm's Owls remain farther north to facilitate quicker repossession through territoriality of a significant rare resource, nest cavities. This life history model may also apply to Northern Saw-whet Owls in North America and could be an important part of any working hypothesis designed to explain the owls migration and wintering in the East.

In most of eastern North America, the breeding range of Northern Saw-whet Owls is characterized by winters with consistent, often deep, snow cover and long periods when temperatures remain well below 0° C. Capturing small mammal prey under these conditions is sufficiently difficult that some populations of Northern Saw-whet Owls may have developed a strategy where females migrate to areas with a milder winter climate, less frequent continuous snow cover and therefore better prey accessibility and potential for owl survival. Theoretically, all species of migratory birds migrate for access to more abundant food. As with Tengmalm's Owl (Koprimaki 1987), more agile and experienced adult male Northern Saw-whet Owls may remain near breeding territories and an important rare resource, nest cavities, to better compete for territories in early spring.

Northern Saw-whet Owls are also frequently preyed upon by larger owls, especially Barred Owls (*Strix varia*) and Great Horned Owls (*Bubo virginianus*) and seem to prefer habitats containing dense thickets where the risk of predation is less. Thus, when deciduous trees lose their leaves each autumn the cover available to Northern Saw-whet Owls in potential wintering areas in the northern and central U.S. decreases dramatically. Coincidentally, at most latitudes in the east, the peak autumn movement of this species usually occurs just as autumn leaf fall is completed. These factors may make migration to coniferous or evergreen shrub habitats an attractive survival strategy for some definable proportion of Northern Saw-whet Owl populations.

Where in eastern North America is there habitat with good cover, mild winter climate, and abundant prey populations? The approximate distribution of the major areas of coniferous forest in eastern North America is illustrated in figure 5. Northern coniferous forests generally coincide with the breeding habitat of Northern Saw-whet Owls. South of the breeding forest lies an area that may represent an ecological desert of farmland and deciduous forest that has little cover during winter. Before settlement, most of this area was either tall grass prairie or mature deciduous forest and thus potentially unsuitable or marginal wintering habitat for this species. Much of this area also has frequent snow cover and regular cold periods. Upon reaching the southern boundary of northern coniferous forests, it is possible that choices to go farther south or remain at the southern edge of the breeding range affect age and sex classes differently. In contrast, the southeastern coniferous forest represents an area that provides cover, food, and a relatively mild, generally snow free climate. Southeastern forests also have understories that contain evergreen shrubs such as laurels (*Kalmia* sp.), various rhododendrons (*Rhododendron* sp.), American Holly, bayberries (*Myrica* sp.) and magnolias (*Magnolia* sp.) that provide cover not present in northern forests during winter. Based upon Holroyd and Woods (1975) and a review of more recent recoveries in the Bird Banding Laboratory data base, most long distance recoveries terminate in the southeastern coniferous forests. Wintering in the south-

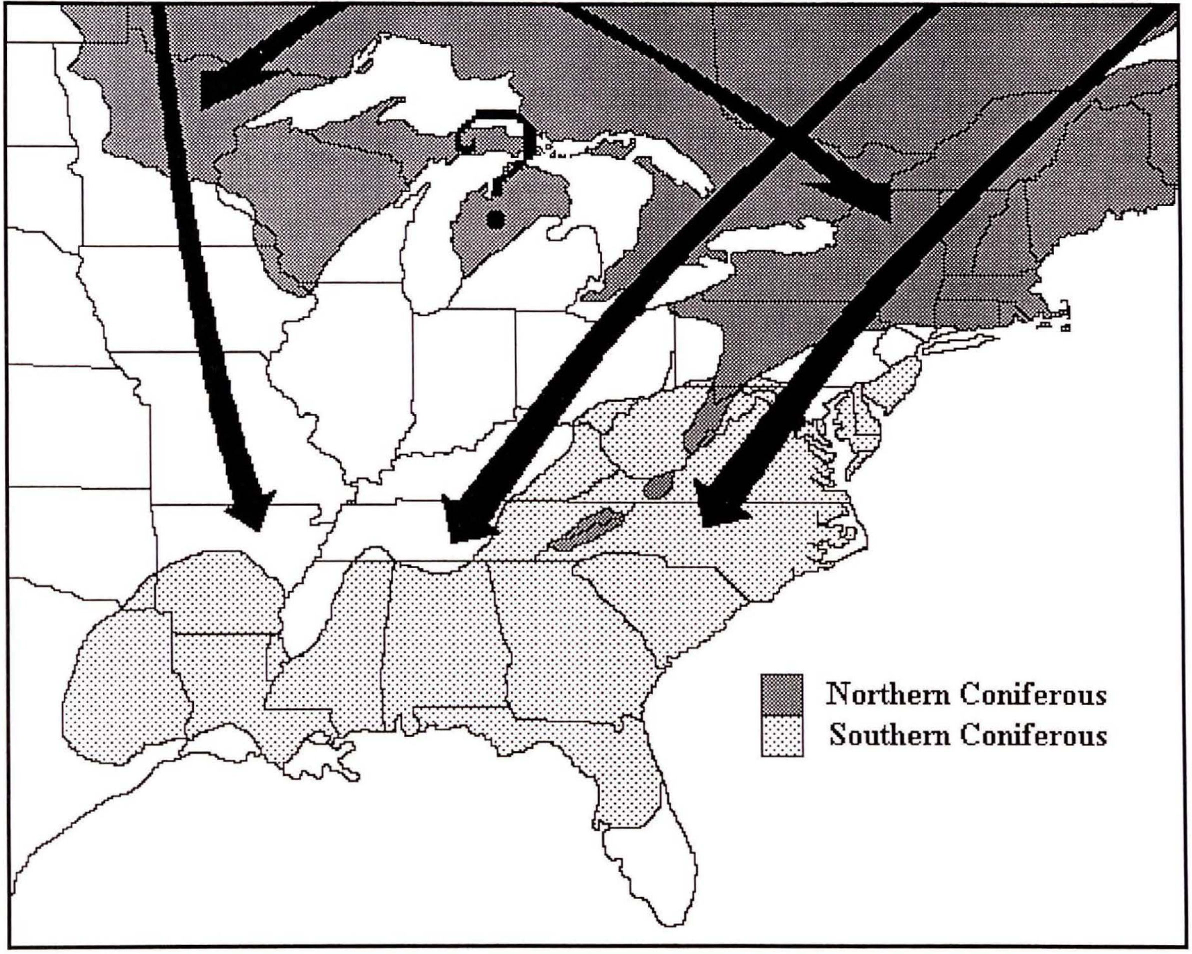

Figure 5.—*Distribution of northern and southern coniferous forest in eastern North America and postulated movement patterns of autumn migrant Northern Saw-whet Owls. Breeding range corresponds closely with the distribution of northern coniferous forest. Wintering individuals have been found as far south as northern Florida. Owls encountered south of 40° north latitude (approximate latitude of Philadelphia, PA) are primarily females. The complex movement patterns around and across the Great Lakes have not yet been described and are represented by a ?.*

eastern forests might represent a successful strategy for female Northern Saw-whet Owls.

Possible pathways between breeding areas in the north and wintering habitat in the southeast are illustrated in figure 5. The movement out of the northeastern U.S. and eastern Canada agrees with recoveries reported in Holroyd and Woods (1975), review of more recent recoveries, and our observations from 1995. Movements from central Canada through the north central U.S. are complicated by the Great Lakes and considerable work remains to be done to better define migratory pathways through the Great Lakes region.

Does this represent a functional hypothesis unifying the observations accumulated over the years that explains some aspects of Northern Saw-whet Owl migration? Only many more years of work from a much expanded network of banding stations will provide the answer.

CONCLUSION

Over the years more than 56,000 Northern Saw-whet Owls have been banded, more than any other owl species in North America, yet we have no unifying framework that summarizes migration as it relates to the life history of the species. Some of this is because of a lack of basic knowledge, such as criteria for determination of sex, and an inadequate network of banding stations. Other questions also beg for answers. What role did prey abundances play in 1995 reproductive success and subsequent autumn migration? Was the early winter weather in central and eastern Canada during 1995 influential in precipitating the Northern Saw-whet Owl flight? Because of these and other knowledge gaps, it is difficult to provide anything more than speculative explanations of the 1995 movement that was documented in the eastern U.S. Without more active banding stations working together throughout the East, it will be difficult to piece together the puzzle of migration mysteries for this intriguing little owl. With recent advances, such as audiolures and a possible method to determine sex in migrants, cooperative regional studies have the potential to begin testing pieces of theoretical frameworks that might describe migration in Northern Saw-whet Owls.

It is time to ask more directed questions of studies on migrant Northern Saw-whet Owls. One place to start would be to see if Korpimaki's model of wintering in Tengmalm's Owls might also apply to the Northern Saw-whet Owl migration and wintering areas in North America. We should begin to test questions related to differential migration. The many Northern Saw-whet Owl banding stations should begin more cooperative analysis of recoveries, retraps and other data from the thousands of owls already banded, as well as the 2,000-5,000 newly banded owls each year.

The ability to effectively conserve any species depends upon adequate knowledge of its life history. Much remains to be learned of Northern Saw-whet Owl migration and winter ecology.

ACKNOWLEDGMENTS

The work reported here has benefited from the volunteer assistance of many individuals across three states. They are too numerous to mention individually, but this would not have been possible without each and every one of them. A variety of institutions: The Nature Conservancy, The Cape May Bird Observatory, Assateague Island National Seashore, Eastern Shore of Virginia National Wildlife Refuge, Kiptopeke State Park, Virginia Department of Game and Inland Fisheries, and Maryland Department of Natural Resources provided support in many ways, including permission to establish banding sites on lands under their control. Funding assistance was provided by the Maryland Ornithological Society, Cape May Bird Observatory, Virginia Department of Game and Inland Fisheries, and the Center for Conservation Biology at the College of William and Mary. The manuscript was improved by the reviews of Eirik A.T. Blom, Thomas C. Erdman, and Matthew P. Rowe. Collectively, we thank you all!

LITERATURE CITED

Barb, M.A. 1995. Natural history of the Northern Saw-whet Owl (*Aegolius acadicus*) in Southern Appalachian Mountains. Johnson City, TN: East Tennessee State University. 68 p. M.S. thesis.

Buckholtz, P.G.; Edwards, M.H.; Ong, B.G.; Weir, R.D. 1984. Differences by age and sex in the size of Saw-whet Owls. Journal of Field Ornithology. 55(2): 204-213.

Davis, T.H. 1966. The 1965 Saw-whet Owl invasion. Kingbird. 16(2): 69-72.

Duffy, K.; Kerlinger, P.A. 1992. Autumn owl migration at Cape May Point, New Jersey. Wilson Bulletin. 104(2): 312-320.

Erdman, T.C.; Brinker, D.F. 1997. Increasing mist net captures of migrant Northern Saw-whet Owls with an audiolure. In: Duncan, J.R.; Johnson, D.H.; Nicholls, T.H., eds. Biology and conservation of owls of the northern hemisphere: 2d international symposium; 1997 February 5-9; Winnipeg, Manitoba. Gen. Tech. Rep. NC-190. U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station: 533-544.

Erdman, T.C.; Meyer, T.O.; Smith, J.H.; Erdman, D.M. 1997. Autumn populations and movements of migrant Northern Saw-whet Owls (*Aegolius acadicus*) at Little Suamico, Wisconsin. In: Duncan, J.R.; Johnson, D.H.; Nicholls, T.H., eds. Biology and conservation of owls of the northern hemisphere: 2d international symposium; 1997 February 5-9; Winnipeg, Manitoba. Gen. Tech. Rep. NC-190. U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station: 167-172.

Evans, D.L. 1997. The influence of broadcast tape-recorded calls on captures of fall migrant Northern Saw-whet Owls (*Aegolius acadicus*) and Long-eared Owls (*Asio otus*). In: Duncan, J.R.; Johnson, D.H.; Nicholls, T.H., eds. Biology and conservation of owls of the northern hemisphere: 2d international symposium; 1997 February 5-9; Winnipeg, Manitoba. Gen. Tech. Rep. NC-190. U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station: 173-174.

Evans, D.L.; Rosenfield, R.R. 1987. Remigial molt in fall migrant Long-eared and Northern Saw-whet Owls. In: Nero, R.W.; Clark, R.J.; Knapton, R.J.; Hamre, R.H., eds. Biology and conservation of northern forest owls: symposium proceedings; 1987 February 3-7; Winnipeg, MB. Gen. Tech. Rep. RM-142. Fort Collins, CO: U.S. Department of Agriculture, Forest Service Rocky Mountain Forest and Range Experiment Station: 209-214.

Fleming, T.L.; Halverson, J.L.; Buchanan, J.B. 1996. Use of DNA analysis to identify sex of Northern Spotted Owls (*Strix occidentalis caurina*). Journal of Raptor Research. 30(3): 118-122.

Holroyd, G.L.; Woods, J.G. 1975. Migration of the Saw-whet Owl in Eastern North America. Bird Banding. 46(2): 101-105.

Kerlinger, P.; Lein, M.R. 1986. Differences in winter range among age-sex classes of Snowy Owls *Nyctea scandiaca* in North America. Ornis Scandinavica. 17(1): 1-7.

Korpimaki, E. 1987. Sexual size dimorphism and life-history traits of Tengmalm's Owl: a review. In: Nero, R.W.; Clark, R.J.; Knapton, R.J.; Hamre, R.H., eds. Biology and conservation of northern forest owls; symposium proceedings; 1987 February 3-7; Winnipeg, MB. Gen. Tech. Rep. RM-142. Fort Collins, CO: U.S. Department of Agriculture, Forest Service Rocky Mountain Forest and Range Experiment Station: 157-161.

Lesser, F.H.; Stickley, A.R., Jr. 1967. Occurrence of the Saw-whet Owl in Florida. Auk. 84(3): 425.

Miller, L.M.; Loftin, R.W. 1984. The Northern Saw-whet Owl in northeast Florida. Florida Field Naturalist. 12(1): 11-12.

Mueller, H.C. 1982. Sexing Saw-whet Owls by wing chord. Wilson Bulletin. 94(4): 554-555.

Mueller, H.C.; Berger, D.D. 1967. Observations on migrating Saw-whet Owls. Bird Banding. 28(2): 120-125.

Reese, J.G. 1966. An unprecedented concentration of Saw-whet Owls. Maryland Birdlife. 22(2): 31.

Slack, R.S. 1992. An unexpected sex ration in a sample of Northern Saw-whet Owls. North American Bird Bander. 17(1): 1-5.

Weir, R.D.; Cooke, F.; Edwards, M.H.; Stewart, R.B. 1980. Fall migration of Saw-whet Owls at Prince Edward Point, Ontario. Wilson Bulletin. 92(4): 475-488.

APPENDIX

Determination of Sex in Northern Saw-whet Owls

Since Weir *et al.* (1980) first published criteria for determination of sex in Northern Saw-whet Owls from wing chord measurements, other authors have commented that the criteria were flawed because observed sex ratios differed from 1:1 (Mueller 1982, Evans and Rosenfield 1987, Slack 1992). During the winter of 1995, blood samples were obtained from eight owls to determine the sex of individuals for a telemetry study of wintering owls on Assateague Island. Using the criteria of Weir *et al.* (1980), as modified by Buckholtz *et al.* (1984), the sample represented three males, four unknown sex individuals, and one female. Blood analysis of DNA (Fleming *et al.* 1996) revealed that the sample actually consisted of eight females (Brinker, unpubl. data). The probability of drawing a random sample of eight individuals of the same sex from a population with a 1:1 sex ratio is 0.0039 and thus we would expect eight females from less than 1 in 100 samples of eight individuals. As has been long suspected and argued, the wing chord method of determining sex for Northern Saw-whet Owls obviously does not work reliably. For this analysis a new approach was pursued to assign sex to individual owls.

A discriminant function (DF) was developed that relied upon a combination of wing chord and mass to assign sex to owls. The training data set consisted of mass and wing chord measurements from 17 live known sex Northern Saw-whet Owls, 6 males and 11 females. Seven were breeding individuals from

Garrett County in western Maryland. One was a female with a brood patch that was captured in a nest box. Two were breeding season males mist-netted during late June and neither possessed a brood patch. Four (two females, two males) were breeding individuals mist-netted at nest boxes. These four were blood sampled to verify use of DNA analysis for sex identification (Fleming *et al.* 1996); the males lacked brood patches and the females possessed brood patches. The remaining 10 were mist-netted in eastern Maryland outside breeding range, during autumn migration of 1996 (two owls) or as winter residents on Assateague during 1996 (eight owls). The sex of these 10 individuals was determined from blood samples. The DF used the within covariance matrix rather than the pooled covariance matrix because the variance structure was significantly different (ä = 0.05) between males and females.

Testing the DF by resubstitution, there were no errors. A better test of the accuracy of the DF was with a second set of data from 20 different known sex individuals, 7 males and 13 females. This set consisted of four breeding owls from the mountains of Tennessee (Barb 1995), 11 road kills collected near Cape Charles during the autumn and winter of 1995-1996 that were sexed internally, and five wintering (1997) Northern Saw-whet Owls from Assateague that were sexed from blood samples. The DF correctly assigned sex to 18 individuals. The two errors were males classified as females. Probability of class membership was used to improve the DF. When probability of membership for both sexes was less than 0.9, the individual was considered unknown sex. This resulted in one of the incorrectly assigned males being assigned to the unknown category and no others changed. The distribution of all training and test owls is shown in figure 6.

The DF performed much better than the old wing chord criteria, which should no longer be used to determine sex in Northern Saw-whet Owls. As an additional test of the DF, consider mass and wing chord data from 35 Northern Saw-whet Owls netted at two eastern Maryland stations during the autumn of 1996 (Brinker, unpublished data). When plotted, there were two distinctly obvious groups of points (fig. 7). The smaller group of points was the lower mass and shorter wing chord group. Two individuals from this group were sexed from blood samples and they were males. If the assumption that

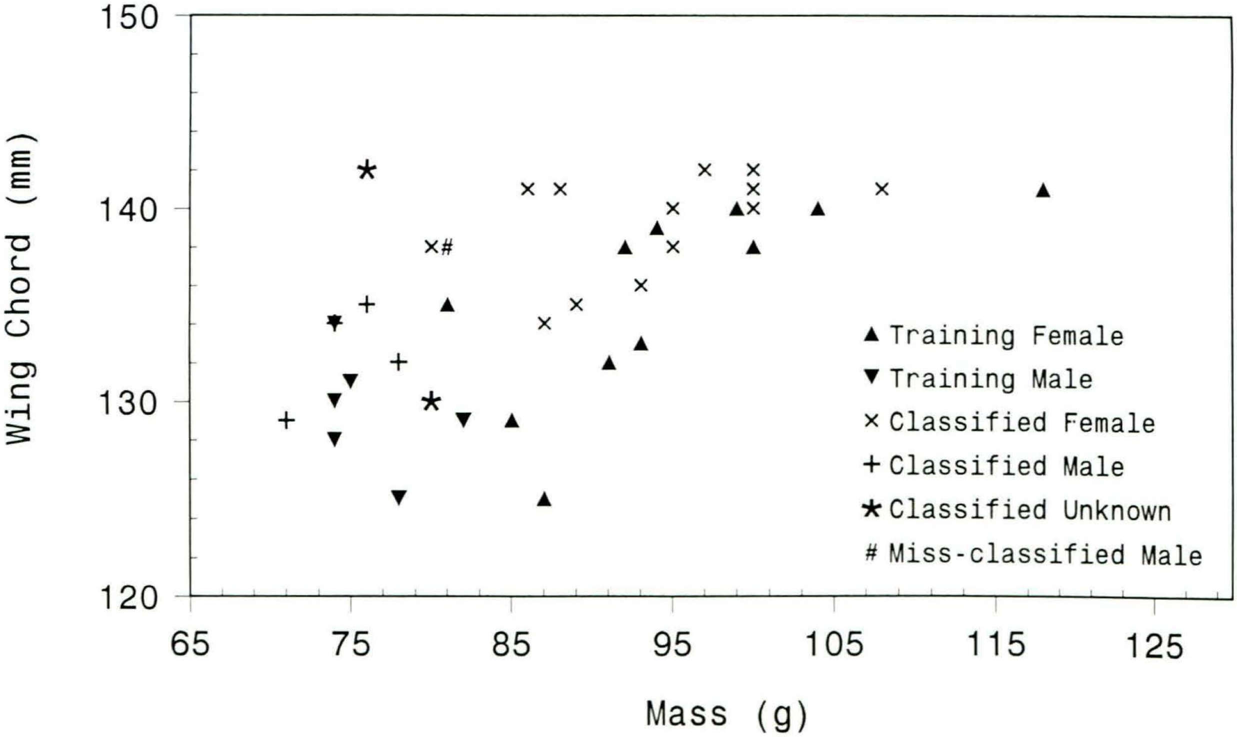

Figure 6.—*Plot of mass vs. wing chord values for individual Northern Saw-whet Owls used to develop and test the discriminant function used to determine sex. Triangles (n=17) represent individuals used for training the DF. All other symbols (n=20) were test individuals.*

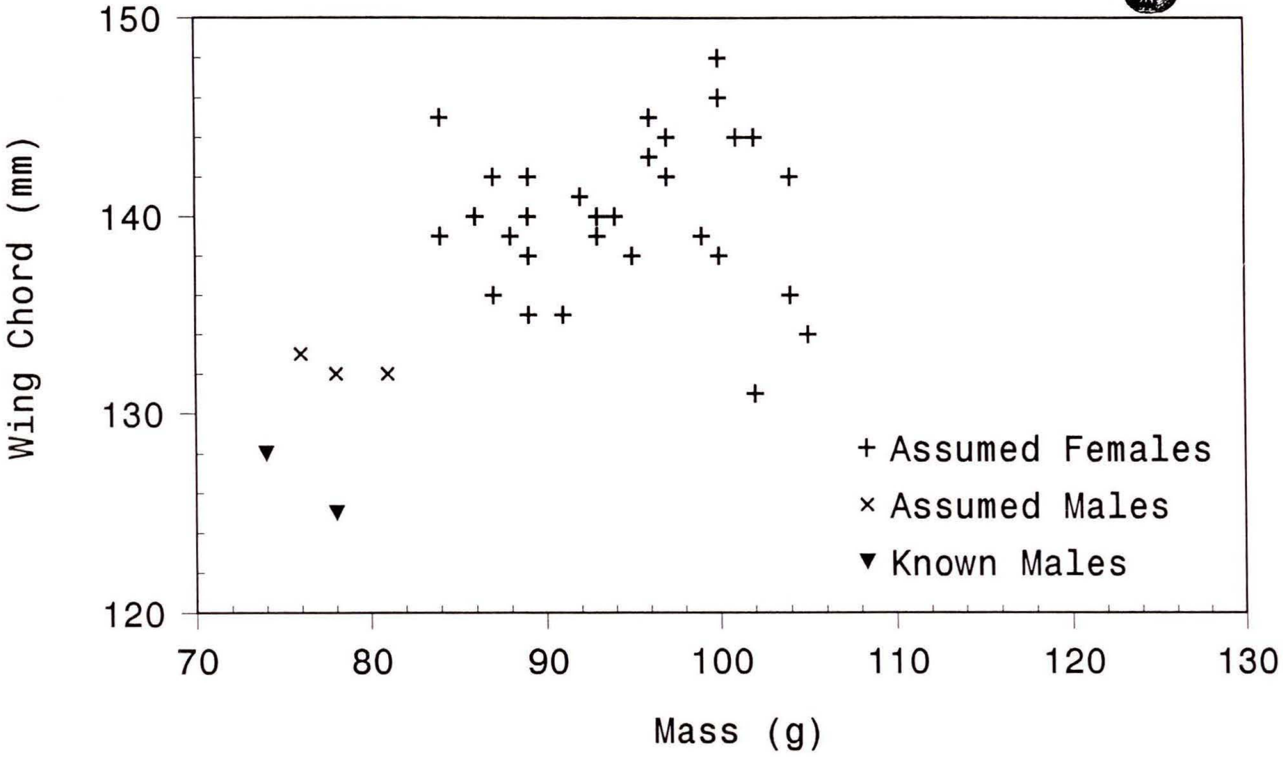

Figure 7.—*Plot of mass vs. wing chord for 35 individual Northern Saw-whet Owls netted during the 1996 autumn migration at two stations in eastern Maryland. The two triangles represent individuals whose sex was determined from blood analysis. In order to test the discriminant function, the sex of all other individuals was assigned. Individuals with masses over 81 g were assigned to female, masses of 81 g or less were assigned to male.*

the two groups represent males and females is pursued further and these data are used to test the DF, all owls are assigned a sex (i.e., using the 0.9 rule no unknowns were assigned) and no assigned sexes deviated from the assumed sex. We state this only to bolster confidence that, for this analysis, the DF is a valid approach to assigning sex.

The female owls that were netted during 1995 were lighter than during more normal years. This is supported by the observation that among all stations and years, the mean mass of immature females was lowest in 1995. Except Assateague, the same was true for adult females. The unusually low mean mass for adult females at Assateague during 1994 may simply be the result of a small sample. For the lighter than usual 1995 females the DF identifies more females as unknowns. However, we do not believe the DF to have erred much in assignment of sex to males and all owls considered females were most certainly correctly classified.

Solely for the purpose of this analysis, the DF was considered adequate and used to assign sex to owls. Those individuals with probabilities of membership for both sexes less than 0.9 were assigned to sex unknown. When more data become available, the use of discriminant analysis to determine sex in Northern Saw-whet Owls will be published elsewhere. Anyone seeking additional information on using this DF for assignment of sex to Northern Saw-whet Owls should contact the senior author.

A Spatial Analysis of the Burrowing Owl (*Speotyto cunicularia*) Population in Santa Clara County, California, Using a Geographic Information System

Janis Taylor Buchanan[1]

Abstract .— A small population of Burrowing Owls (*Speotyto cunicularia*) is found in the San Francisco Bay Area, particularly in Santa Clara County. These owls utilize habitat that is dispersed throughout this heavily urbanized region. In an effort to establish a conservation plan for Burrowing Owls in Santa Clara County, a spatial analysis of owl distribution and habitat was performed using remote sensing and geographic information system (GIS) technologies. Land areas that could provide valuable habitat for owls in the future and that could link together groups of owls throughout the region, were identified.

The Burrowing Owl (*Speotyto cunicularia*), a grassland species, utilizes open sparsely vegetated areas with available burrows (Zarn 1974). Historically, owls were common in natural areas of open prairies or in shrub-steppe habitat (Butts 1971, Coulombe 1971). Increasing human population and land use changes have caused Burrowing Owls to utilize man-altered habitats, such as agricultural irrigation ditches (Coulombe 1971) and vacant lands in urban areas (Thomsen 1971, Collins and Landry 1977, Wesemann and Rowe 1987, Trulio 1995). Burrowing Owls are tolerant of humans near their burrows, given suitable nesting and foraging habitat (Trulio 1992).

Nesting and foraging habitat requirements for the Burrowing Owl include sparse vegetative cover, availability of suitable burrows typically built by fossorial mammals, and the presence of perches that provide increased visibility. The amount of vegetative cover and overall plant height are significant factors in predator avoidance and prey location (Zarn 1974, Coulombe 1971, Green and Anthony 1989, Trulio 1992). In general, vegetative cover and height that allow the owl to stand near the burrow entrance and watch for approaching predators from any direction is most desirable. Burrows built and abandoned by fossorial mammals are taken over by Burrowing Owls throughout most of its North American range, excluding Florida, where Burrowing Owls dig their own burrows (Zarn 1974). The burrow provides protection from both predators (Green and Anthony 1989, Butts 1971) and adverse weather conditions (Coulombe 1971), and creates a microhabitat for arthropods (such as earwigs and crickets), which may form the owls' primary food source (Coulombe 1971). Perches adjacent to the burrow entrance increase visibility for the Burrowing Owl while it watches for predators or prey (Green and Anthony 1989).

The Burrowing Owl is considered a rare animal throughout most of its range. In Minnesota, Iowa, and Canada, it is listed as an endangered species. In California, Florida, Montana, North Dakota, Oregon, Washington, and Wyoming, the Burrowing Owl is listed as a species of special concern (Martell 1990). The Burrowing Owl has been on the *Journal of American Birds*' blue list since 1971 (Arbib 1971), which indicates that bird researchers identify it as a declining species. The California Department of Fish and Game listed the Burrowing Owl as a "Species of Special Concern" in 1979 due to declining populations throughout the State (Remsen 1978). In November 1994, the U.S. Fish and Wildlife Service classified the Burrowing Owl as a federal Category 2 candidate for listing as threatened or endangered. Additional evidence (DeSante and Ruhlen, unpubl. data) has shown that this species is unquestionably at risk throughout California.

In California, distribution of the Burrowing Owl is not uniform. There are an estimated 9,450 pairs of Burrowing Owls within the State

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(DeSante and Ruhlen, unpubl. data). Seventy-one percent of the breeding pairs of owls can be found in the Imperial Valley, 14 percent are in the southern Central Valley, and 14 percent are distributed throughout the San Francisco Bay area, middle and northern Central Valley and southern interior portions of the State. Flat, lowland valleys, basin bottoms, and coastal plains are the habitat of 90 percent of breeding Burrowing Owls in California (DeSante and Ruhlen, unpubl. data). These lowland areas, in addition to supporting the greatest number of breeding pairs of owls, have also been subjected to the greatest human population growth throughout the 1980's and early 1990's, particularly in the San Francisco Bay area and Central Valley locations (DeSante and Ruhlen, unpubl. data, Medvitz and Sokolow 1995).

The focus of this study is Santa Clara County, in the San Francisco Bay Area. It was a major agricultural center 30 years ago. Thousands of acres of farmland existed across the valley floor with some of the richest agricultural soil in the world. However, the 1970's brought explosive human population growth to the county. Today, over half the valley floor in Santa Clara County is developed (Bell *et al.* 1994). Within the last century, at least 90 percent of the County land in agriculture was abandoned, and for the most part, urbanized (Faye *et al.* 1985).

The Burrowing Owl population in Santa Clara County represents a window into the future of the remaining owl habitat throughout California. Urbanization represents a permanent loss of available habitat for the species, and this small population of owls is surrounded by urbanization with very few options for long-term protection.

The Institute for Bird Populations (IBP) conducted a census of Burrowing Owls in California from 1991-1993. The findings of the IBP study indicate a population decline greater than 50 percent in the last decade (DeSante and Ruhlen, unpubl. data). Today there are approximately 170 pairs of owls in the south San Francisco Bay Area (fig. 1). Most of the owls in this area utilize undeveloped or limited use lands throughout the urban matrix. Nesting populations of Burrowing Owls have been extirpated in the past 15 years from several counties in and around the San Francisco Bay Area, including Santa Cruz, Marin, and San Francisco, and nearly eliminated from several others.

Human population growth predictions indicate the population of California will double its current level by the year 2040 (Medvitz and Sokolow 1995). The Imperial Valley and the southern Central Valley are among the fastest growing regions within the State. In the Imperial Valley, the population is increasing by 3.6 percent per year and San Joaquin Valley's population is increasing by 2.5 percent per year. These increases are directly linked to the loss of agricultural lands due to urban expansion (Medvitz and Sokolow 1995). By the year 2040, the predicted loss of agricultural land in California is expected to be 5 million acres (2.02 million ha), or 17 percent of today's farmland base. Urbanization directly impacts Burrowing Owls because over 85 percent of the Burrowing Owl population in California is found on agricultural land in the Central Valley (DeSante and Ruhlen, unpubl. data).

In this study a geographic information system (GIS) was used to spatially link nest locations to current land uses across the entire Santa Clara County creating a landscape perspective for the evaluation of Burrowing Owl habitat protection. A landscape perspective is essential because habitat protection requires all cities within the county to participate equally in the protection of the species. In Santa Clara County, the conservation of Burrowing Owls and availability of habitat can't be solved by relying on each city to develop an individual habitat protection plan. Some cities have more owls and less habitat available for the future, while others have more habitat available but fewer owls.

Knowledge of owl locations and habitats that are most likely to be lost to development in the coming years is critical in the development of mitigation plans that offset the environmental impacts of development. Mitigation plans can include conservation easements or mitigation banks to define best available habitat without the limitation of city boundaries. Successfully protecting owl habitat in Santa Clara County in the future relies upon understanding where owls are found, how development will change available habitat in the future, and which lands are most appropriate to protect to ensure a viable population.

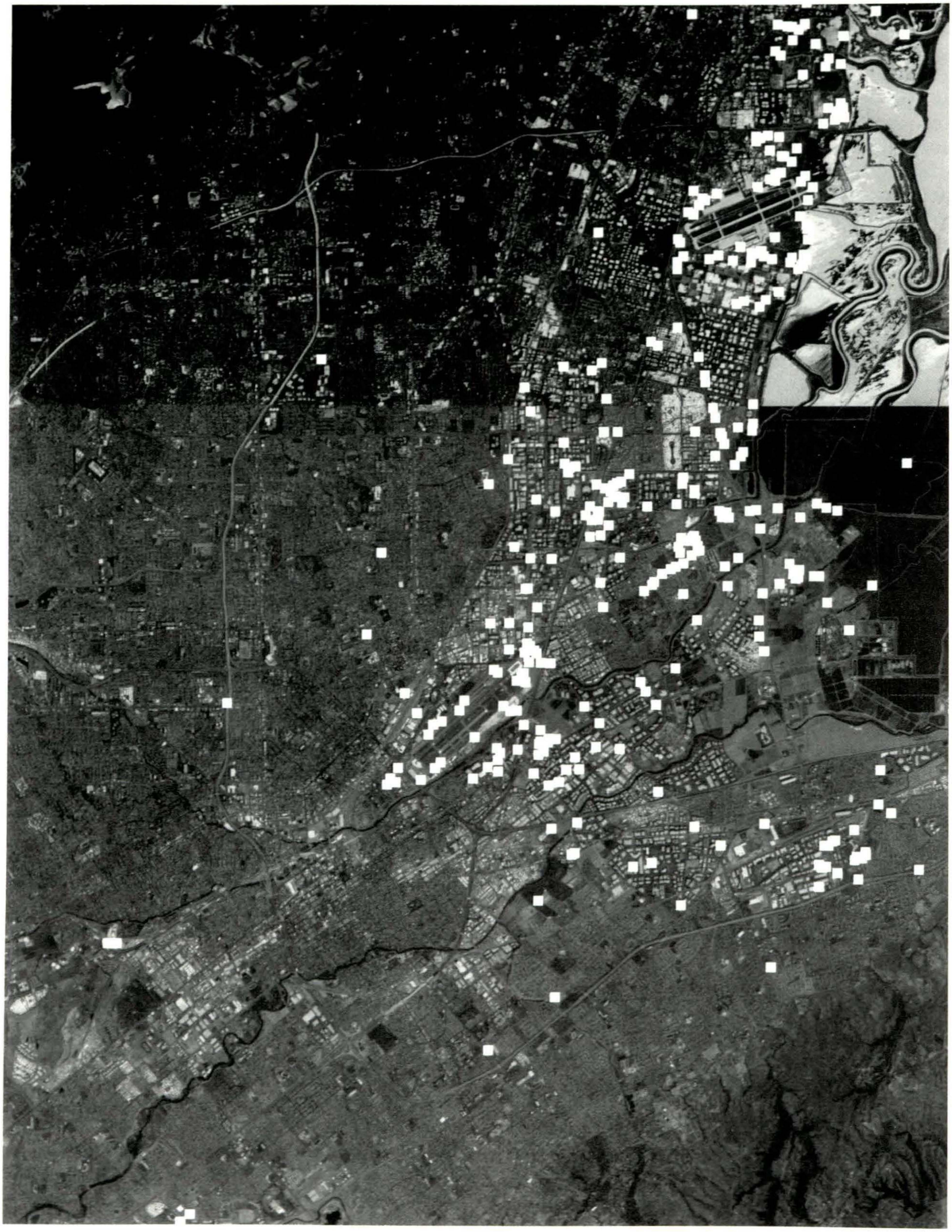

Figure 1.—*This image is a composite of SPOT satellite images dated May 1994 and May, June 1994. The south end of San Francisco Bay can be seen at the top of this image. Overlaid on the image are owl locations shown as white squares. These locations are from census data for the years 1991-1994. Each point identifies a nesting burrow with one or more owls at each point.*

The IBP census of Burrowing Owls revealed that the decline in the state-wide population was approximately 8 percent per year (DeSante and Ruhlen, unpubl. data). It was also estimated that 50 percent of the population of Burrowing Owls in the State was lost from 1985-1995. The owl is still broadly distributed throughout the State and occupies a variety of habitats, but small local populations (like the one in the San Francisco Bay area) may have limited long-term viability unless the population is increased and a permanent system of protected areas is established (DeSante and Ruhlen, unpubl. data; Trulio, unpubl. data).

GIS and Remote Sensing

Ecosystem management requires information on many system components and their interactions in the landscape, at different spatial scales. Modeling landscapes and species distribution with GIS and remotely sensed data has relieved researchers of difficult and time-consuming processes involving traditional cartographic methods. Integration of diverse databases, spatial analysis, and a final map product are all benefits of using a GIS. Utilization of a GIS in ecosystem management makes recording and spatial analysis of the data time-efficient, while creating the environment for a flexible visualization process to display complex relationships.

GIS demonstrated its utility in the development of a reserve design for the Northern Spotted Owl (*Strix occidentalis*) (Murphy and Noon 1992). Four primary map layers were compiled to spatially display information relevant to the species' ecology. The first layer represented species distribution at a scale dependent on species level response to environmental variation and the spatial extent of environmental disturbances. Map layer number two contained the distribution of historical and present locations of suitable habitat, including disturbed areas that had the potential of recovery to suitable habitat. The third map layer consisted of survey and census data on the Northern Spotted Owl. Land ownership and use patterns made up the final map layer. The intersection of all four map layers became the initial conservation map representing a starting point in the design of a reserve system for the Northern Spotted Owl. Pertinent biological variables were applied to this initial map to create different map patterns. Additional iterations of maps were statistically analyzed in the development of a final map product which is considered a scientifically valid approach to the development of a conservation reserve for the Northern Spotted Owl.

This study of Burrowing Owls and their habitat in Santa Clara County follows a methodology similar to that described above. Several map layers, including census data, historical data on the population, and land ownership, were combined in the context of a plan for protection of Burrowing Owls and their habitat in Santa Clara County. This study differs from Murphy and Noon in that less is known about Burrowing Owl demographics and distribution than Spotted Owls, and the study focuses on "basemap" information. Important information is compiled on owl distribution in relation to habitat type and land uses, and potential Burrowing Owl habitat and owl reserves are identified. This study forms a foundation on which Burrowing Owl conservation plans can be developed.

METHODS

Remote sensing, in conjunction with GIS, were the tools for this study. Three data sets were used to analyze Burrowing Owls and their habitat use in Santa Clara County, California. Population data from the IBP and local researchers provided locations of owls within the study area. A Landsat Thematic Mapper (TM) image was classified and combined with owl location data to analyze habitat use within the study area. A land use data set from the city of San Jose was overlaid on the classified image with owl locations to identify potential owl habitat areas which should be protected.

Study Site

Santa Clara County is located in northern California, at the southern end of San Francisco Bay. It is a broad, flat valley surrounded by the Santa Cruz Mountains to the west, the Diablo Range to the east, and San Francisco Bay to the north. This study focused on the central portion of Santa Clara County, approximately 730 km^2 of the valley floor. Current land uses within the study area include industrial, residential, commercial, open space, and vacant land. Intermixed within all of these land uses is a Burrowing Owl population of approximately 170 breeding pairs (DeSante and Ruhlen, unpubl. data; Trulio, unpubl. data).

Burrowing Owl Location Data

When the IBP censused Burrowing Owls in California during the years 1991-1993, all potential habitat was included in their census except for the Great Basin and desert areas in southern California. IBP divided the State into 1,835 census blocks that were 5 km x 5 km. Each 5 km x 5 km block was extracted from a 7.5 minute topographic map and this became the data sheet where volunteer census takers recorded owl locations during the Burrowing Owl nesting season, May 15 to July 15. An owl location is where one or more owls are observed at a burrow.

In preparation for the census, the IBP gathered information on the historical locations of Burrowing Owls for the years 1986-1990 from breeding bird surveys, Christmas bird counts, and mitigation studies. In addition to the historical and census data from IBP, this study utilized 1994 owl location information from local researchers. These researchers included Dr. L. Trulio, P. Delevoryas, Biosystems Analysis Incorporated, and the author.

All geographic locations of Burrowing Owls in Santa Clara County, historical records for the years 1986-1990, census records from the IBP for the years 1991-1993, and local census information for the year 1994, were digitized as points using ARC/INFO GIS software, v. 7.0 (ESRI 1994). Five georeferenced data layers were generated representing historical locations (pre-1991) of owls and the 4 years (1991-1994) of census data. Each point was attributed with the year it was referenced, the map sheet number, and a specific location number recorded in the census for that location.

Habitat Classification

A June 20, 1990, Landsat TM scene (path 44, row 34, ID 52302-18061), which includes the San Francisco Bay Area, was used to characterize six categories of land cover. The image, in its raw data format, was registered to a 30-m Universal Transverse Mercator (UTM) grid using corner and center coordinates supplied by EOSAT (C. Bell, NASA/Ames 1993). A subset of the full Landsat scene, which included over 95 percent of the known owl locations in Santa Clara County (both past and present) was made by excluding land above 250 ft (76 m) in elevation. Lands over this elevation were eliminated based on information gathered by the IBP which showed that 98 percent of the Burrowing Owls in Santa Clara County occupied sites below 200 ft (61 m) in elevation. The southern-end of the Santa Clara County, including the towns of Morgan Hill and Gilroy, had very few reported sightings of Burrowing Owls, and was not included in the study.

The software program "Spectrum" was used to classify the six of the seven TM bands in the Landsat image. The seventh TM band, thermal, was excluded from this analysis. Spectrum, developed by Los Alamos National Laboratory, pre-processes the raw data utilizing intrinsic properties from each of the six bands. Raw spectral data were grouped into 240 clusters using a nearest-neighbor algorithm, creating a smaller, more compressed, data set while retaining the integrity of the original spectral data. Each pixel in the original six-band image was assigned to one cluster. The output was a single-band image, called a clustered image. The 240 clusters were then grouped into six categories of land cover defined for this study.

The six land cover categories included water, developed land, bare soil, dense vegetation, dry grassland, and irrigated grassland. Of these six categories, emphasis was placed on dry and irrigated grasslands, habitat owls were most likely to be utilizing. The final product, a classified landsat image with six defined land cover classes, was colored coded for identification.

Spatial Analysis of Burrowing Owl Locations

A spatial analysis of the owl locations included interpretation of distribution patterns over time. Five GIS data layers, one for each year (pre-1991, 1991-1994), consisted of a point for each owl location. Maps generated from these five data layers were compared to one another visually. Polygons were drawn around groups of owl locations based on criteria from studies done by the IBP and Trulio (unpubl. data): groups of five or more locations in a single habitat area have a much lower chance of extinction and all existing large colonies should be maintained intact in the future. Stochastic environmental factors such as drought or prey reduction are likely to eliminate a small group of birds (DeSante and Ruhlen, unpubl. data; Trulio, unpubl. data).

Burrowing Owl Habitat Analysis

The amount of area was calculated for each of the six land cover categories. Since dry and irrigated grassland provided the greatest amount of available habitat for Burrowing Owls in Santa Clara County, the amount of this habitat type was calculated at each owl location, within 90 m buffers around each owl location, and within the polygons around groups of five locations or more.

Future Land Use

An analysis of potential future habitat or reserves for the Burrowing Owl in parts of Santa Clara County was conducted by evaluating the location of owls with respect to potential habitat and future development throughout the cities of San Jose and Santa Clara. Visual inspection, in conjunction with information about land ownership, was used to evaluate whether the known owl locations within the city of Santa Clara were protected from habitat loss in the future. Future habitat in the city of San Jose was also evaluated. This was accomplished by overlaying the vacant lands inventory, a projection of land uses for currently vacant and agricultural lands, from the city of San Jose. Projections were made about how habitat for Burrowing Owls could be increased in the northern portions of San Jose by mitigating development of open or agricultural land with Burrowing Owl habitat. Projected development throughout the study area was considered with respect to the impacts on Burrowing Owls in the future.

RESULTS

A visual analysis of the distribution change in Burrowing Owls over the study period showed a decrease in the number of owls and a concentration of the remaining owl locations. Nearly all of the Burrowing Owls currently residing in the study area can be found within a thin band around the south end of San Francisco Bay and in a ribbon of habitat running south, from the Bay through the San Jose airport. Moreover, owls are concentrated in habitat patches. The decline in owls and their habitat was confirmed by a ground inspection of all pre-1991 locations by Trulio and Buchanan in 1995. This inspection revealed that over 60 percent of the pre-1991 locations had been replaced by development. Conversion of dry grassland into developed land is the main reason for this population decline throughout the cities of San Jose, Santa Clara, Sunnyvale, Milpitas, and Mountain View.

Areas in which larger groups of owls are located can be considered protected habitat based solely on current land use and land management practices. For example, Burrowing Owls that reside on San Jose airport property, located mostly in San Jose, or Moffett Field Naval Air Station in Mountain View (the property includes an airfield), have a much greater chance of long-term survival because land utilization on these properties is not expected to change significantly in the future. The dry grass habitat at these locations is mowed several times per year, creating an environment that is conducive to a large number of Burrowing Owls. Management of the airport maintains nesting habitat away from runways, preserving both owls and public safety.

Owls located on public land, such as owls at Sunnyvale Baylands Park and Shoreline, are more likely to survive in the future, where both nesting and foraging habitat is actively protected.

RECOMMENDATIONS

Because Burrowing Owls are found in all cities in Santa Clara County, county action or collective city action is required to protect the owl population. There is no one single development project that will decimate the population, but incremental losses of habitat have a cumulative impact on the number of owls and will eventually result in a population too small for survival (Trulio, unpubl. data).

Compilation of information about Burrowing Owls in Santa Clara County using GIS creates a dynamic data set. Information about land use changes and new population census data can be added at any time, setting the stage for on-going analysis of population change. Utilization of remotely sensed data allows efficient evaluation of large land areas. This study has established a baseline of information about Burrowing Owls in this urban region and can be used to develop a conservation strategy that will protect the birds for the future. It is also a model for protection of Burrowing Owl habitat in other areas where urbanization is having an impact.

ACKNOWLEDGMENTS

This study was a Master's Thesis for the Environmental Studies Department at San Jose State University in San Jose, California, completed December 1996. The work was completed in the Ecosystem Science Division's GIS laboratory at NASA Ames Research Center. Future updates to the data in the GIS will be conducted by the author in order to continue the analysis of the Burrowing Owl population in Santa Clara County.

LITERATURE CITED

Arbib, R. 1971. Announcing—the blue list: "an early warning system" for birds. American Birds. 25: 948-949.

Bell, C.; Acevedo, W.; Buchanan, J.T. 1994. Dynamic mapping of urban regions: growth of the San Francisco Sacramento Region. In: Proceedings, 3d Annual urban and regional information systems association conference; 1995 July 16-20; San Antonio, TX: 723-734.

Butts, K.O. 1971. Observations on the ecology of Burrowing Owls in western Oklahoma. A preliminary report. Proceedings of the Oklahoma Academy of Science. 51: 66-74.

Collins, C.T.; Landry, R.E. 1977. Artificial nest burrows for Burrowing Owls. North American Bird Bander. 2: 151-154.

Coulombe, H.N. 1971. Behavior and population ecology of the Burrowing Owl, Speotyto cunicularia, in the Imperial Valley. Condor. 73: 162-176.

Faye, J.S.; Lipow, A.G.; Faye, S.W., eds. 1985. California almanac. San Francisco, CA: Presidio Press and Pacific Data Resources.

Green, G.A.; Anthony, R.G. 1989. Nesting success and habitat relationships of Burrowing Owls in the Columbia Basin, Oregon. The Condor. 91: 347-354.

Martell, M.S. 1990. Reintroduction of Burrowing Owls into Minnesota: a feasibility study. St. Paul, MN: University of Minnesota. M.S. thesis.

Medvitz, A.; Sokolow, A.D. 1995. Population growth threatens agriculture, open space. California Agriculture. 49(6): 11-15.

Murphy, D.D.; Noon, B.R. 1992. Integrating scientific methods with habitat conservation planning: reserve design for Northern Spotted Owls. Ecological Applications. 2(1): 3-17.

Remsen, J.V., Jr. 1978. Bird species of special concern in California: an annotated list of declining or vulnerable bird species, California. Proj. PR W-54-R-9, Rep. #78-1. Sacramento, CA: Department of Fish and Game.

Thomsen, L. 1971. Behavior and ecology of Burrowing Owls on the Oakland airport. Condor. 73: 177-192.

Trulio, L.A. 1992. Burrow borrowers. Pacific Discovery. 45: 19-21.

Wesemann, T.; Rowe, M. 1987. Factors influencing the distribution and abundance of Burrowing Owls in Cape Coral, Florida. In: Adams, L.W.; Leedy, D.L., eds. Integrating man and nature in the metropolitan environment. Proceedings, National symposium on urban wildlife. Baltimore, MD: Urban Wildlife Press.

Zarn, M. 1974. Burrowing Owl. Tech. Note T-N-250. Denver, CO: U.S. Department of the Interior, Bureau of Land Management. 25 p.

Modeling Critical Habitat for Flammulated Owls (*Otus flammeolus*)

David A. Christie and Astrid M. van Woudenberg[1]

Abstract.—Multiple logistic regression analysis was used to produce a prediction model for Flammulated Owl (*Otus flammeolus*) breeding habitat within the Kamloops Forest Region in south-central British Columbia. Using the model equation, a pilot habitat prediction map was created within a Geographic Information System (GIS) environment that had a 75.7 percent classification accuracy. Factors were identified indicating the quality of the modeling process; several limitations were also detected. Maps derived from the pilot model will be ground-truthed in coordination with field inventories. New habitat identified from the field investigations will be used to refine models in an ongoing, iterative process.

BACKGROUND AND RATIONALE

Operational planning requirements of the Forest Practices Code of British Columbia Act and the corresponding Regulations include the protection of critical habitat for species at risk within resource development plans (Ministry of Forests 1995). Geographic Information Systems (GIS) may be used to efficiently map critical habitat features allowing for integrative mapping and analysis within logging and development plans. Unfortunately, collecting adequate data to detect and map habitat for all species at risk would be an exhaustive process.

British Columbia has the highest level of biodiversity of any province in Canada (Harding and McCullum 1994, Pojar 1993). The Kamloops Forest Region is representative of the Province's diversity. The Biogeoclimatic Ecosystem Classification (BEC) system of British Columbia has divided the province into 14 broad zones, 10 of which are present in the Kamloops Forest Region (Lloyd *et al.* 1990). These 10 zones span the climatic spectrum from dry, hot desert climate to pockets of high elevation, coastal rain forest. Inherent in the diversity of ecosystems is the diversity of wildlife. Increasing human disturbance in these ecosystems has led to a significant number of species recognized as being at risk (Harding and McCullum 1994).

Using traditional methods for mapping habitat over extensive regions is costly, time consuming, and labor intensive (Stefanovič and Wiersema 1985). The difficulty of the task in the Kamloops Forest Region is exacerbated by steep and complex terrain and extensive dense forests. Predictive habitat modeling has been recognized as a practical alternative to traditional surveys for some time (Anderson *et al.* 1980, Carneggie 1970, Carneggie *et al.* 1983, Christie and Low 1996, Hunter 1990). Star and Estes (1990) described GIS as the only practical method for predictive habitat modeling for rare, threatened and endangered species in California. Potential critical wildlife habitat in British Columbia may be modeled using GIS database variables such as forest cover characteristics, terrain, and juxtaposition of critical habitat features. Models could be used to produce maps of potential habitat which may efficiently guide field inventory studies.

Several factors have delayed the acceptance of predictive habitat modeling over a planning area as large as the Kamloops Forest Region (6.7 million ha (Watts 1983)). First, legislated requirements for critical habitat mapping applied consistently over the entire region and to all resource planners did not, until recently, exist. Second, the scope of many early GIS-based habitat modeling studies was often restricted by data limitations such as inappropriate data resolution (scale), data cost, and data quality and precision (Herr and Queen 1993, Lyon 1983, Pétrie 1990, Stefanovič and Wiersema 1985). These limitations, combined with inadequate budgets, consequently

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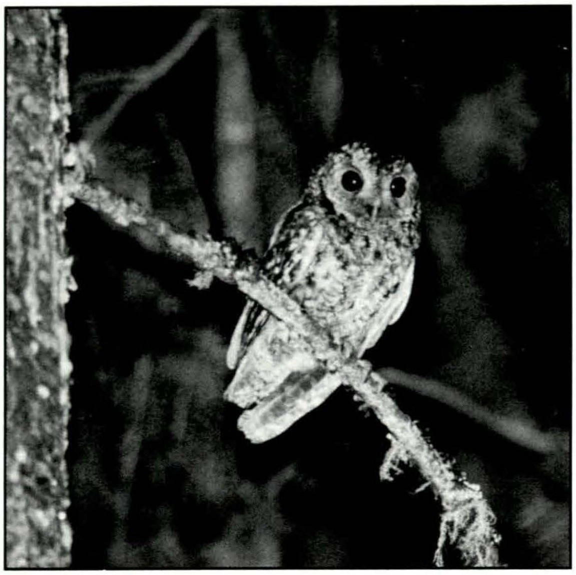

David A. Christie

*Adult Flammulated Owl (*Otus flammeolus*).*

produced moderately successful results. Finally, failing to weight different habitat variables relative to their importance to a species was also cited as a reason for limited success in habitat modeling (Lyon 1983).

Recent studies have met with more favorable results. Pereira and Itami (1991) modeled habitat for the endangered Mt. Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*) in Arizona using various abiotic (terrain) and biotic (vegetation) variables. The model successfully classified 90 percent of squirrel habitat and only misclassified 27 percent of the non-habitat. Duncan *et al.* (1995) used multitemporal data to validate their Florida Scrub Jay (*Aphelocoma coerulescens coerulescens*) habitat suitability model. Habitat prediction modeling for wolves (*Canis lupis*) in Peter Lougheed Provincial Park, Alberta, also produced excellent results (Waters 1996). Sperduto and Congalton (1996) used the results of chi-square analysis to weight habitat variables and increase the modeling accuracy for a rare orchid (*Isotria medeoloides*) in New Hampshire and Maine. All project teams benefited from combined GIS and wildlife expertise. Unfortunately, results of these studies are only applicable to the study areas in question due to the use of site-specific data.

Hunter (1990) suggested that plans based on GIS and remote sensing data require careful scrutiny by wildlife managers to recognize the deficiencies of the modeling process. Conversely, wildlife managers who venture into GIS modeling must also seek the scrutiny of GIS experts. Too often, habitat models have failed to produce adequate results because they were developed either by wildlife biologists with inadequate GIS experiences or GIS modelers with insufficient knowledge of wildlife and wildlife habitat.

STUDY SITE AND SPECIES DESCRIPTION

The Flammulated Owl (*Otus flammeolus*) is a neotropical migrant and summer resident in British Columbia where it nests primarily in woodpecker cavities in ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*) snags (Cannings *et al.* 1987, Howie and Ritcey 1987, van Woudenberg unpubl. data). At 15 to 18 cm tall and weighing approximately 55 grams, it is the second smallest owl in North America (McCallum 1994). The owl is nocturnal and secretive, foraging in small grassy openings for Lepidopterans, Othopterans and Coleopterans.

Wheeler Mountain was the trial study site where Flammulated Owl habitat research had been conducted from 1989 to 1996 (fig. 1). The forest is mature to old growth (80-200+ years), with Douglas-fir as the dominant species and ponderosa pine as a subdominant on xeric, south aspect sites of the Mountain (van Woudenberg, unpubl. data). Predominant species in the shrub layer include Saskatoon

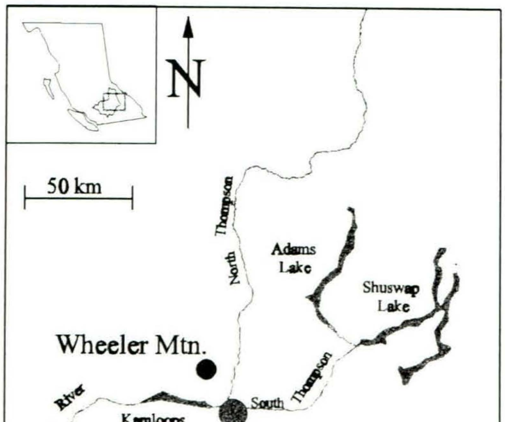

Figure 1.—*Location of Wheeler Mountain pilot study site, British Columbia, Canada.*

(*Amelanchier alnifolia*), birch-leaved spirea (*Spirea betulifolia*), common snowberry (*Symphoricarpos albus*) and soopolalie (*Shepherdia canadensis*). Kinnikinnick (*Arctostaphylos uva-ursi*) is the dominant forb, and pinegrass (*Calamagrostis rubescens*), rough fescue (*Festuca scabrella*), and bluebunch wheatgrass (*Agropyron spicatum*) are the dominant graminoids.

The transition between mesic and xeric sites, where large ponderosa pine snags are found near stands of Douglas-fir regeneration and small grassy openings, is optimal habitat for the Flammulated Owl (van Woudenberg, unpubl. data). The Douglas-fir regeneration provides foraging opportunities and security cover, the openings provide foraging opportunities and snags are used as nest sites. Douglas-fir snags are used more often for nesting in mesic sites where ponderosa pine is minimal or absent. Where ponderosa pine is scarce, suitable nesting may be the limiting habitat type for Flammulated Owl populations. In xeric sites, where ponderosa pine snags are more common, security cover may be the limiting habitat feature. This may be mitigated by reduced risk of predation on xeric sites (van Woudenberg, unpubl. data). Generally, nest cavities in ponderosa pine are created by Pileated Woodpeckers (*Dryocopus pileatus*) and cavities in Douglas-fir are created by Northern Flickers (*Colaptes auratus*).

METHODS

The first stage of research focused on the pilot study site, an approach recommended by Star and Estes (1990) for two reasons. First, field data collected from the study site would allow preliminary testing of proposed methods and experimental design. Second, the relevance of different data types may be investigated during the trial study before committing to large data acquisitions.

The Ministry of Environment supplied 1:20,000 scale Terrain Resource Information Management (TRIM) digital map data to be used as the base. A Triangulated Irregular Network (TIN) Digital Elevation Model (DEM) was created from TRIM spot elevation data. The Kamloops Region Ministry of Forests (MoF) provided 1:20,000 scale forest cover maps and database files. All nest site locations collected from the pilot site were derived using differential Global Positioning System (GPS). A CMT MC5-GPS unit (Corvallis Microtechnology Inc. 1995) was used for field data collection.

TerraSoft V.10.03 (Digital Resource Systems Ltd. 1991) was used for GIS input and analyses. A combined theme containing polygons with all variables was created through theme overlay processes. Thirty-five nest sites, found between 1989 and 1995, were used for model calibration. A total of 29 polygons were used as some polygons contained multiple nest sites. Due to the large number of eligible polygons (approx. 20,000) in the Flammulated Owl habitat database and the small number of polygons with owl nests, a case-control sampling with complete sampling of cases and random sampling of controls was performed. The significant contributions of each variable to characterize habitat was tested by comparing polygons containing documented habitat features with randomly chosen polygons without known habitat features.

The independent variables considered were slope, elevation, aspect, primary, and secondary tree species and their respective percentages, age class, crown closure (percent), and site index (forest productivity). A filter was applied to select only polygons with Douglas-fir as the primary species for two reasons. First, all polygons with nests had Douglas-fir as the primary species. Second, this filter excluded non-forested and water feature polygons from the modeling process. Polygons were also filtered to exclude erroneous polygons with elevations less than the lowest elevation on the source map.

After completing the univariate analyses, variables were selected for multivariate analysis. The problem with the univariate approach is that it ignores the possibility that a collection of variables that may be weakly associated with the outcome can become an important predictor when considered together. Due to the complexity of the problem in this study, it was decided that the stepwise logistic regression would be used to select variables for the final model. The technique used in the stepwise logistic regression was forward variable selection with a test for backward elimination. The following hypotheses was tested for the pilot model:

H_0: There is no significant lack of fit of the model.

H_A: There is a significant lack of fit of the model.

79To test this hypotheses, the final model was tested for goodness of fit within a 95 percent confidence interval using the Hosmer-Lemeshow goodness of fit test (Hosmer and Lemeshow 1989). The model was then used to query the database for polygons with predicted habitat suitability; a map identifying those polygons was produced.

RESULTS

Polygons containing nest sites ranged in elevation from 850 to 1,150 m, 10 to 50 percent slope, and all aspects were represented except north. The dominant tree species for all polygons was Douglas-fir and percentage cover was from 55 to 100. Ponderosa pine was the secondary species for 19 nest sites and it ranged in percentage cover from 3 to 45; lodgepole pine (*Pinus contorta*) was the secondary species for two nest sites where it comprised 5 and 40 percent, respectively. There were no secondary species for the remaining 14 nest sites. The age class ranged from 5 to 8, crown closure from 30 to 50 percent, and site index from 8.5 to 15.6.

The significant predictor variables included ELEV_01, a binary variable for elevation (ELEV_01 = 0 if <900m and >1,100m, ELEV_01=1 if >= 900m and <= 1,100m). The other significant predictor variables were AGE_CLASS, specifically older stands, and CROWN_CLOS, typically 40-50 percent, or that of an older stand. P-values for each significant variable were well below the 0.05 significance level.

The final model equation was;

$$Y = -11.63 + 2.22*ELEV\_01 + 0.58*CROWN\_CLOS + 0.11*AGE\_CLASS$$

The probability of finding a nest in the predicted forest polygon was calculated by:

$$p = 1/[1 + EXP(-Y)]$$

Using the model equation, a pilot habitat capability map was created within the GIS environment having a 75.7 percent classification accuracy (optimum probability limit of 0.35) (fig. 2). The coefficients and standard errors of final model variables are shown in table 1.

Table 1.—*Coefficients and standard errors of final model predictor variables.*

Variable	Coefficient	Standard error
Intercept	-11.6341	2.9527
ELEV_01	2.2197	0.7849
AGE_CLASS	0.5822	0.2420
CROWN_CLOS	0.1083	0.0360

DISCUSSION

Several factors indicated the quality of the modeling process. The higher standard deviation values for the randomly selected polygons without confirmed nesting indicated that a broad range of non-nested or control polygons were used to generate the prediction model. Because the coefficient values are all greater than zero, each variable was positively associated with habitat suitability. The predictor variables derived through development of the model were available from forest cover and TRIM maps, and were therefore readily available for all areas of concern. Furthermore, the independent variables selected to derive the habitat suitability prediction model were biologically meaningful to Flammulated Owl nesting habitat and were highly associated with this habitat.

The small sample size of polygons with nest sites (n=33) affected the power of the multivariate analysis. For example, the variables that were excluded from the prediction model, site index and slope, may be important features for owl nests but were not analytically detected in the few polygons with documented nests. As the nest inventory work continues on Wheeler Mountain and surrounding sites, more samples will be available for the modeling process. For example, the 1996 project detected 13 new nest sites whose locations are now available for habitat modeling, bringing the sample size to 46. After each year of inventory, and with expanded inventory sites, the efficiency of the model should improve.

Since the nesting data used to derive the model was extracted using a point in polygon overlay, it is questionable whether this data is a good representation of the species' home range. Most polygons are considerably smaller than the estimated 3.0 ha home range size on Wheeler Mountain (van Woudenberg, unpubl.

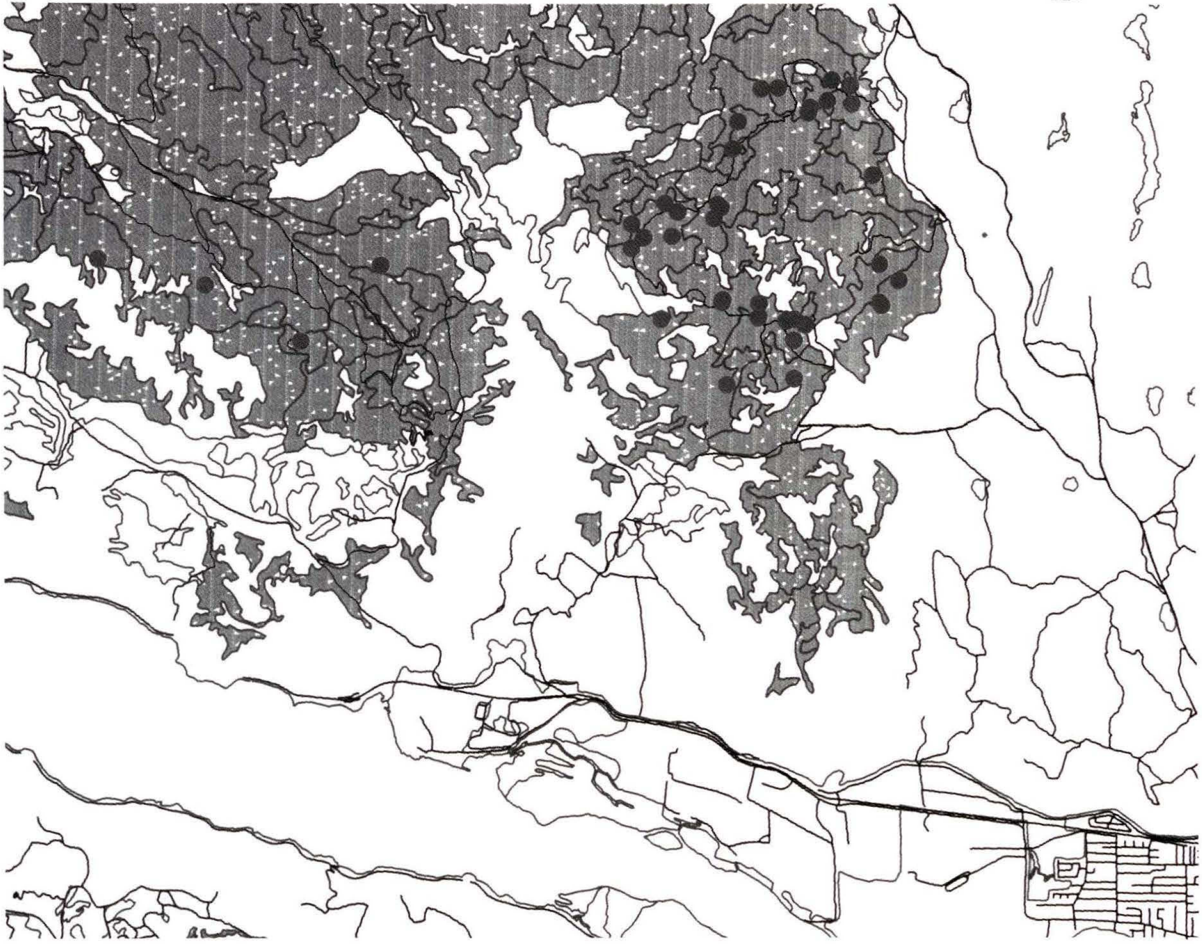

Figure 2.—*Predicted habitat for Flammulated Owls for the 1:20,000 scale forest cover map which encompasses the Wheeler Mountain study site, British Columbia. The shaded forest cover polygons are areas of predicted habitat. Circles represent documented nest site locations. The map also shows the northeastern outskirts of the city of Kamloops in the lower right corner.*

data). It would therefore be wise to refine the model using polygon overlays that are more representative of the home range. This would likely improve model accuracy by ensuring that adjacent polygons are not used as non-nesting polygons during model development and testing.

The data analysis used to generate the model did not include spatial relationships such as distance between nest sites which may be indicative of the owl's home range size. The distance between nest sites and water bodies and large openings may also be important. The owls tend to avoid large water bodies and riparian areas, likely due to their intolerance of humidity (McCallum 1994). The owls also seem to avoid nesting within several hundred meters of large openings (>1 ha), probably to reduce the risk of predation. Using a GIS buffering operation, buffers could be placed around riparian areas and large openings to exclude these features from predicted habitat.

The superiority of the Triangulated Irregular Network (TIN) elevation model for representing irregular terrain surfaces has been well documented (Burrough 1986, Peucker *et al.* 1978). For terrain modeling purposes, the collection of spot elevation data points should be dictated by the relief of the surface being modeled. TRIM map spot elevations were collected in a uniform grid pattern which did not reflect the terrain complexity of the mapping area. This terrain mapping will suffice for some purposes but may be inadequate for representing subtle terrain conditions that indicate the presence of critical habitat features. This has necessitated the investigation of surrogate elevation data sources.

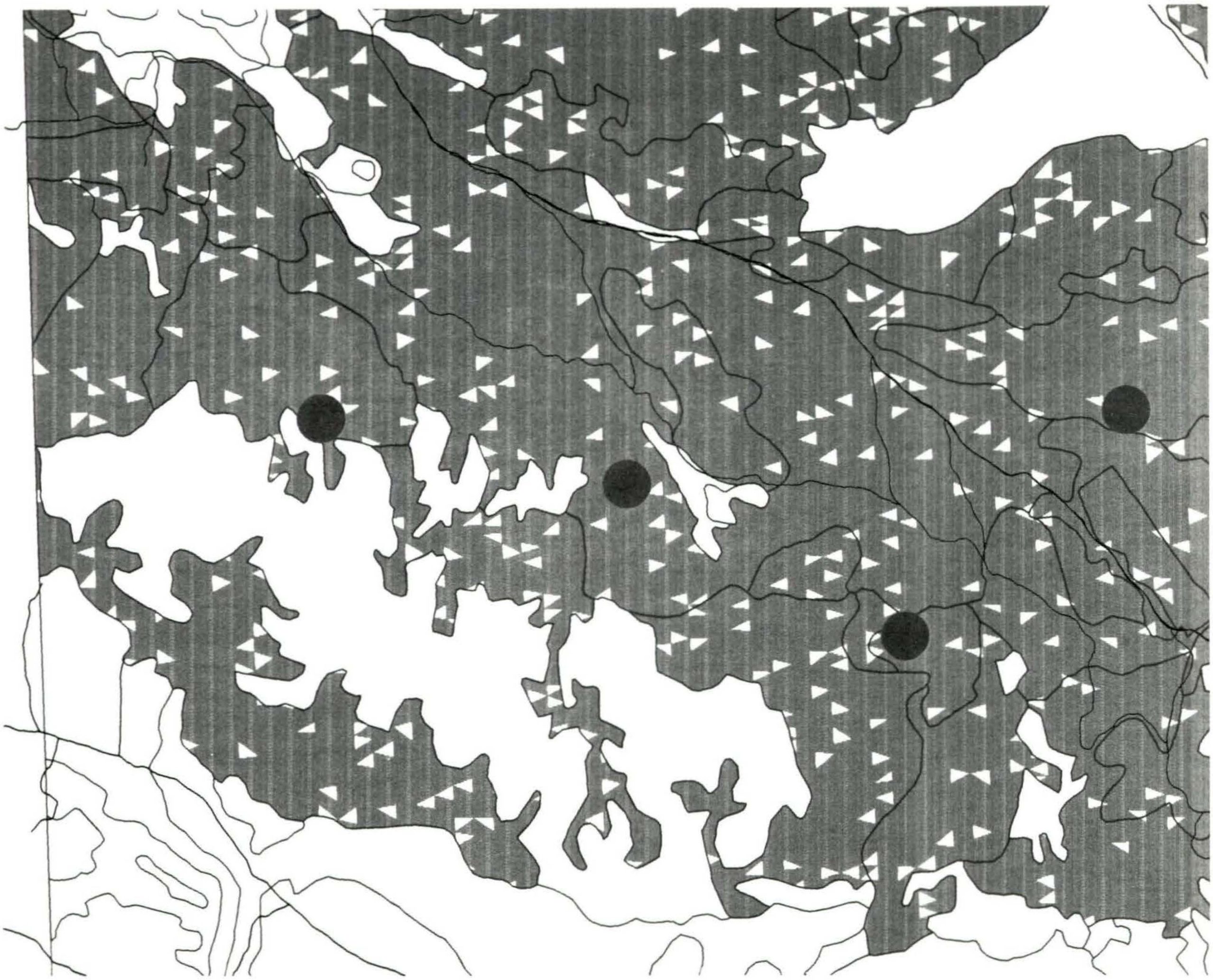

Figure 3.—*This portion of the pilot map shows an overgeneralized forest cover polygon at the Wheeler Mountain study site, British Columbia. This polygon contains the second nest from the left (circle). This nest site is located in a Douglas-fir dominated portion of the polygon while the remainder of the polygon is dominated by lodgepole pine unsuitable as habitat for Flammulated Owls. The triangles within polygons are also unsuitable Flammulated Owl habitat.*

Perusal of the final map identified problems with overgeneralized forest cover polygons based on the modeler's knowledge gained from field surveys in those sites. For example, one forest cover polygon covered a very large area and incorporated a variety of distinct stands of trees (fig. 3). The polygon was classed as 40 percent lodgepole pine cover. The area within the polygon where nesting occurred was large enough to constitute a separate polygon and contained 100 percent Douglas-fir cover. The polygon had been overgeneralized, perhaps by an inability of the photointerpreter to detect the differences in the forest cover. The problem is unavoidable for forest cover mapping when map makers lack field knowledge of the area and conditions being mapped. The problem may be ameliorated by relevant practical knowledge by the modeler or modeling team.

Temporally static data (sampled from a single period in time) is a potential downfall of many wildlife habitat models (Pereira and Itami 1991, Hodgson *et al.* 1987). Data collection replicated through time is necessary for proper identification of annual and seasonal habitat differences and occurrence of periodic fluctuations which affect a species' choice of habitat. Vernier *et al.* (1993) addressed the danger of classifying habitat based on one year's potentially atypical data. For example, Flammulated Owls in the Kamloops area may have responded to outbreaks of western spruce budworm (*Choristoneura occidentalis*) as an opportunistic food supply (van Woudenberg, unpubl. data). Sampling habitat during a single year of heavy outbreak may lead to classifying habitat that can be less productive in non-outbreak years. Productive habitat and habitat types shift with changing conditions, something that is impossible to detect without long-term studies.

Although habitat data has been collected from the Wheeler Mountain site for 6 years, the majority of the nest sites found to date were located between 1994 and 1996 (34 of 46 or 74 percent). The summer of 1994 was extremely hot and dry in the Kamloops area. The spring of 1995 was unseasonably mild and the summer was wetter than normal; the spring and summer of 1996 were colder and wetter than most recorded years (Dave Low, pers. comm.). These differences affected both the spatial distribution of nesting and the nesting success of the owls. It could be a costly mistake to assume that the sites detected in these years are completely representative of Flammulated Owl habitat use over time. Data collected over a longer time frame is necessary to obtain a range of habitat use over time.

Measuring habitat during one season may fail to detect habitat that is critical during other seasons. Van Horne (1983) identified social interactions within wildlife populations as a potential habitat classification problem. For some population structures, dominant breeding animals exclude more numerous, sub-dominant, non-breeding animals from highest quality habitat. Classification of habitat based solely upon density of animals, such as results from aural census for Flammulated Owls, would result in a model which identifies sub-optimal habitat as critical at the exclusion of optimal habitat. Protecting only sub-optimal habitat would negatively influence the breeding success and overall stability of the population.

The 75.7 percent classification accuracy of the Flammulated Owl habitat model was surprising because the model relied almost exclusively on forest cover variables. The absence of slope and aspect in the regression model was highly conspicuous. Terrain is perhaps the most significant determinant of wildlife habitat (Stefanovič and Wiersema 1985), particularly for areas with high relief. Pereira and Itami (1991) found slope, elevation and aspect to be statistically significant variables for their Mt. Graham red squirrel habitat model. The predominance of terrain variables occurred even though an equal number of vegetation variables were tested. Pereira and Itami suspected that the vegetation variables, determined to be critical from field research, were not detectable at the coarse resolution of the surrogate data used to model them. The importance of data resolution for detecting critical habitat features was also discussed by Stefanovič and Wiersema (1985) for their Ibex (*Capri ibex*) habitat model in the European Alps.

There is no explicit information regarding the spatial distribution of trees within forest cover polygons, although limited information may be implied from stocking density, volume, etc. Critical habitat variables that were too small to warrant classification as separate polygons, and were consequently grouped into a generalized polygon, present difficulties for modeling. Satellite imagery may also be used to supplement forest cover data for the Flammulated Owl habitat model. Stands with unique forest cover textures, where Flammulated Owl nest sites were most often found during nest site surveys, have been detected using aerial photographs. This texture, lost within a forest cover polygon, represents dense forest patches interspersed by openings <1 ha. The thicket and opening pattern indicates the juxtaposition of critical foraging and security habitat for the owl (van Woudenberg, unpubl. data). The introduction of RADARSAT's Synthetic Aperture Radar (SAR) 10 m resolution imagery to the modeling process should facilitate the detection of the small forest opening and dense patch pattern indicating Flammulated Owl habitat.

For an area as large as the Kamloops Forest Region, remotely sensed data is the only practical approach to uniform data collection. Data suitable for wildlife habitat modeling may be interpreted from aerial photographs or derived from satellite imagery (Stefanovič and Wiersema 1985). Remotely sensed variables may be used as surrogates for desired, high resolution variables if statistical correlations are established (Burrough 1986). Several other new data sources are now available such as 1 m resolution multispectral satellite imagery, sub-meter resolution aerial multispectral imagery and aerial laser topographic imagery.

High resolution digital orthophotographs are another possible source of data which are ideal for many GIS applications (Star and Estes 1990). While this data is more expensive to acquire per unit area, its possible utility for various different planning purposes should make it cost effective at the detailed planning level.

Habitat selection is a species-specific process where habitat features are chosen to meet life requisites. For example, a Flammulated Owl may, as first priority, select suitable foraging habitat before searching for a suitable snag or tree for nesting (van Woudenberg, unpubl. data). Lyon (1983) used separate sub-models to represent different biotic variables and their spatial relationships relative to habitat selection by American Kestrels (*Falco sparverius*) in Oregon. These sub-models were weighted according to their relative importance to the habitat being selected. Equal weighting of variables does not priorize habitat features according to life requisites and will inevitably lead to reduced model accuracy. In summary, Lyon (1983) suggested several conditions necessary for successful modeling of wildlife habitat:

1. model components [variables] must be quantifiable and have biological significance for the species to be studied;
2. the contribution of each sub-model must represent the relative importance of each habitat characteristic for the species;
3. field data must be available to develop the weights (train the model), and for verifying model sensitivity with the known characteristics of the species-preferred habitat; and
4. the land-cover types important to the species must be detectable from the remotely sensed data employed for the study.

The need for sub-models will be determined in part by the species' home range size and by the heterogeneity of its habitat. Flammulated Owl home range size at its northern range limit is relatively small, approximately 3.0 ha (van Woudenberg, unpubl. data), allowing nesting, foraging and security habitat to be modeled as one unit. If a species uses distinctly different habitat types over a large home range then it may be necessary to create several sub-models for that species' habitat. Careful consideration should also be given to infrequently used habitats which, although utilized for less than a few weeks out of the year, may be critical for the long-term sustainability of the species.

CONCLUSIONS

The pilot Flammulated Owl habitat prediction model was completed with promising results. A project team has been assembled with the relevant expertise, training, and experience to contribute to further success of the model. Several model limitations were identified and potential solutions will be applied to future models. The need to detect seasonal and annual variations in habitat and habitat selection necessitate a multi-year project duration. For habitat models to be effective they must address habitat as a dynamic entity. These models must possess the flexibility to adapt to both the habitat they represent and the growing body of habitat knowledge. The essence of this concept has been expressed by Harding and McCullum (1994) in *Biodiversity in British Columbia: Our Changing Environment*:

> "We have been reminded again and again of how much there is yet to learn about the biodiversity of our province. And even as we learn, identifying new species and tracing ecological relationships, the ecosystems around us are changing."

ACKNOWLEDGMENTS

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LITERATURE CITED

Anderson, W.H.; Wentz, W.A.; Treadwell, B.D. 1980. A guide to remote sensing information for wildlife biologists. In: Schemnitz, S.D., ed. Wildlife management techniques manual, 4th ed. (rev.), Chapter 18. Washington, DC: The Wildlife Society: 291-303.

Burrough, P.A. 1986. Chapter 6: Data quality, errors and natural variation. In: Principles of geographical information systems for land resource assessment. New York, NY: Oxford University Press Inc.: 103-135.

Cannings, R.A.; Cannings, R.J.; Cannings, S.G. 1987. Birds of the Okanagan Valley, British Columbia. Victoria, BC: The Royal British Columbia Museum: 202-219.

Carneggie, D.M. 1970. Remote sensing: review of principles and research in range and wildlife management. In: Range and wildlife habitat evaluation - a research symposium; 1970 May. Misc. Publ. 1147. Washington, DC: U.S. Department of Agriculture, Forest Service: 165-178.

Carneggie, D.M.; Schrumpf, B.J.; Mouat, D.A. 1983. Rangeland applications. In: Colwell, R.N.; Simonette, D.S.; Ulaly, F.T.; Estes, J.E.; Thorley, G.A., eds. Manual of remote sensing. Falls Church, VA: American Society of Photogrammetry and Remote Sensing: 2325-2384.

Christie, D.A.; Low, D.J. 1996. Threatened and endangered wildlife and the forest practices code. In: Heit, M.; Parker, H.D.; Shortreid, A., eds. GIS applications in natural resources 2. Fort Collins, CO: GIS World Books: 414-423.

Corvallis Microtechnology Inc. 1995. MC-GPS user's manual. Version 2.4. Corvallis, OR: Corvallis Microtechnology, Inc.

Digital Resource Systems Ltd. 1991. TerraSoft reference guide. Nanaimo, BC: Digital Resource Systems Ltd. (Now owned by PCI Pacific, Victoria, BC). 325 p.

Duncan, B.W.; Breininger, D.R.; Schmalzer, P.A.; Larson, V.L. 1995. Validating a Florida Scrub Jay habitat suitability model using demography data on Kennedy Space Center. Photogrammetric Engineering and Remote Sensing. 61(11): 1361-1370.

Harding, L.E.; McCullum, E., eds. 1994. Biodiversity in British Columbia: our changing environment. Canadian Wildlife Service, Environment Canada. 426 p.

Herr, A.M.; Queen, L.P. 1993. Crane habitat evaluation using GIS and remote sensing. Photogrammetric Engineering and Remote Sensing. 59(10): 1531-1538.

Hodgson, M.E.; Jensen, J.R.; Mackey, H.E., Jr.; Coulter, M.C. 1987. Remote sensing of wetland habitat: a wood stork example. Photogrammetric Engineering and Remote Sensing. 53(8): 1075-1080.

Howie, R.R.; Ritcey, R. 1987. Distribution, habitat selection, and densities of Flammulated Owls in British Columbia. In: Nero, R.W.; Clark, R.J.; Knapton, R.J.; Hamre, R.H., eds. Biology and conservation of northern forest owls: symposium proceedings; 1987 February 3-7; Winnipeg, Manitoba. Gen. Tech. Rep. RM-142. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest Experiment Station.

Hosmer, D.W; Lemeshow, S. 1989. Applied logistic regression. New York, NY: Wiley.

Hunter, M.L. 1990. Wildlife forests and forestry: principles of managing forests for biological diversity. Englewood Cliffs, NJ: Prentice-Hall Inc.: 264-270.

Lloyd, D.; Angove, K.; Hope, G.; Thompson, C. 1990. A guide to site identification and interpretation for the Kamloops Forest Region. Land Manage. Handb. 23. Victoria, BC: British Columbia Ministry of Forests, Research Branch. 399 p.

Lyon, J.G. 1983. Landsat-derived land-cover classifications for locating potential Kestrel nesting habitat. Photogrammetric Engineering and Remote Sensing. 49(2): 245-250.

McCallum, D.A. 1994. Review of technical knowledge: Flammulated Owls. Chapter 4. In: Hayward, G.D.; Verner, J., eds. Flammulated, Boreal, and Great Gray Owls in the United States: a technical conservation assessment. Gen. Tech. Rep. RM-253. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest Experiment Station: 2-86.

Ministry of Forests. 1995. Draft Operational Planning Regulation, Forest Practices Code of British Columbia Act, Victoria, BC: British Columbia Ministry of Forests.

Pereira, J.M.; Itami, C.; Itami, R.M. 1991. GIS-based habitat modelling using logistic multiple regression: a study of the Mt. Graham Red Squirrel. Photogrammetric Engineering and Remote Sensing. 57(11): 1475-1476.

Pétrie, G. 1991. Chapter 4: Photogrammetric methods of data acquisition for terrain modeling. In: Pétrie, G.; Kennie, T.J.M., eds. Terrain modelling in surveying and civil engineering. New York, NY: McGraw-Hill, Inc.: 26-48.

Peucker, T.K.; Fowler, R.J.; Little, J.J.; Mark, D.M. 1978. The triangulated irregular network. In: Proceedings; American society of photogrammetry: digital terrain models (DTM) symposium; 1978 May 9-11; St. Louis, MO: 516-540.

Pojar, J. 1993. Terrestrial diversity of British Columbia. In: Fenger, M.A.; Miller, E.H.; Johnson, J.F.; Williams, E.J.R., eds. Our living legacy: proceedings of a symposium on biological diversity. Victoria, BC: Royal British Columbia Museum: 177-190.

Sperduto, M.B.; Congalton, R.G. 1996. Predicting rare orchid habitat (small whorled pogonia) habitat using GIS. Photogrammetric Engineering and Remote Sensing. 62(11): 1269-1279.

Star, J.; Estes, J. 1990. Geographic information systems: an introduction. Englewood Cliffs, NJ: Prentice-Hall Inc. 303 p.

Stefanovič, P.; Wiersema, G. 1985. Insolation from digital elevation models for mountain habitat evaluation. ITC Journal. 3: 177-186.

van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management. 47(4): 893-901.

Vernier, L.A.; Mather, M.H.; Welsh, D.A. 1993. Density and productivity measures for evaluating habitat quality: implications for wildlife management. In: GIS'93 symposium proceedings: 7th annual symposium on Geographic Information Systems in forestry, environment, and natural resources management; 1993 February 15-18; Vancouver, BC: 518-522.

Waters, N. 1996. A GIS-based prediction model for wolf (Canis lupis) habitat use in Peter Lougheed Province Park, presented by Shelley Alexander at GIS'96, the 10th Annual symposium on Geographic Information Systems for environmental, natural resources and land information management, 1996, March 18-21, Vancouver, BC.

Watts, S.B., ed. 1983. Forestry handbook for British Columbia. 4th ed. Vancouver, BC: The Forestry Undergraduate Society, Faculty of Forestry, University of British Columbia. 125 p.

Burrowing (*Speotyto cunicularia*) Owl Survival in Prairie Canada

Kort M. Clayton and Josef K. Schmutz[1]

Abstract.—We studied survival of the endangered Burrowing Owl (*Speotyto cunicularia*) using radio-telemetry in both Alberta and Saskatchewan. Adult females exhibited the highest mean survival (0.83) whereas adult male (0.46) and juvenile (0.48) rates were similar. Most mortality occurred during the post-fledging period when there was a peak of activity around the nest. The greatest mortality from vehicle collisions occurred in a fragmented agricultural landscape where predation was also the lowest. Our survival estimates, along with other considerations, suggest that low annual survival is potentially limiting Burrowing Owl populations on the Canadian prairies.

Burrowing Owls (*Speotyto cunicularia*) appear to be declining throughout their U.S. and Canadian range. Range constriction and population declines prompted an 'endangered' classification in 1995 by the Committee on the Status of Endangered Wildlife in Canada.

Despite being a relatively well-studied species, few efforts have explicitly addressed survival. This project was initiated to examine post-fledging Burrowing Owl ecology, to include survival, with the hope of illuminating possible limiting factors for this species on the Canadian prairies.

STUDY AREAS AND METHODS

In 1995 and 1996 field work was conducted in southeastern Alberta near the town of Hanna (51°39'N, 111°56'W). Land use in this region is dominated by ranching (<20 percent cultivation). Annual precipitation averages 33 cm. Vegetation is dominated by needle-and-thread (*Stipa comata*), blue grama (*Bouteloua gracilis*), and wheat grasses (*Agropyron* spp.).

The project was expanded in 1996 to include a study area in southeastern Saskatchewan, centered on Milestone, SK (50°00'N, 104°30'W). This area is hereafter referred to as "Regina", as this is the nearest major center. In sharp contrast to the Hanna study area this region has productive agricultural soils and nearly 90 percent of the land surface under cultivation for cereal crops. Annual average precipitation is 38 cm. Wheat grasses and June grass (*Koeleria macrantha*) dominate the native flora.

A total of 16 adult males, 14 adult females, and 46 juvenile owls were radio-tagged during the course of this project. Adults were trapped near the nest from late incubation onwards using bal-chatris and noose carpets. Juveniles were similarly captured once they were old enough to emerge from the burrow. Both adults and juveniles were equipped with 4 g necklace style radio-transmitters in the 172 MHz range from either Holohil Systems Ltd. (Woodlawn, Ontario, Canada) or Merlin Systems Inc. (Meridian, ID, USA).

Both ground and aerial tracking were employed to monitor Burrowing Owls. All frequencies were relocated daily if possible, but typically only every second or third day from the time transmitters went on (late June) until the last owl left the study area (mid October). Remains of casualties were scrutinized to determine the date and cause of death following Einarsen (1956) and Hamerstrom (1972).

Survival and cause-specific mortality estimates were generated using software produced and discussed by Heisey and Fuller (1985). These estimates are based on the total number of radio-days' per time period and are similar to 'Mayfield estimates'. The three survival periods; pre-fledging, post-fledging dependency, and dispersed juveniles, are based on nest chronology and juvenile development.

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RESULTS

Daily survival rates are presented for adult males, adult females, and juveniles through the three survival periods (figs. 1, 2, & 3). In Hanna 1995, no females died and all mortality of males and juveniles occurred during the post-fledging period (fig. 1). In Hanna 1996, all juvenile mortality occurred during the post-fledging period and there was no mortality in any group after dispersal of the juveniles (fig. 2). Most mortality occurred during the post-fledging period in Regina 1996 and again no females died (fig. 3).

Survival and cause-specific mortality rates for the entire study period in each area are given in table 1. Survival of adult males and juveniles are similar among years and areas (36 to 60 percent). Radio-tagged adult females

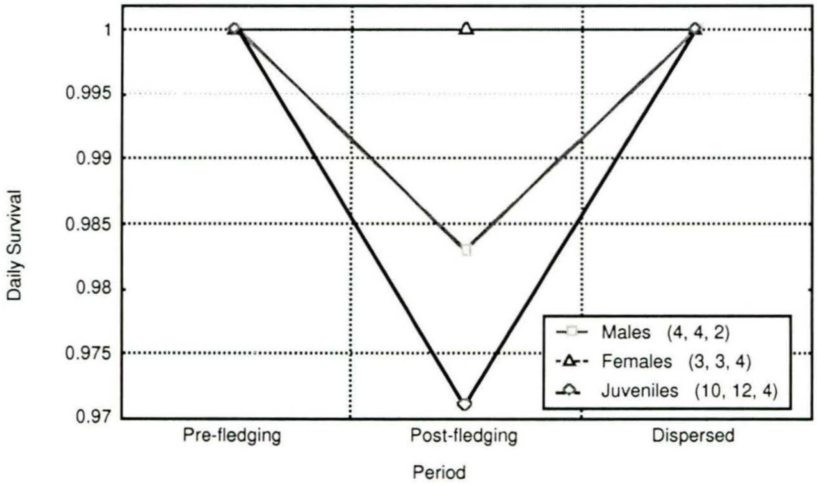

Figure 1.—*Daily survival rates for Burrowing Owls in Hanna, AB 1995. Rates are plotted separately for adult males, adult females, and juveniles across three time periods. Sample size is given in the legend for each time period (chronologically).*

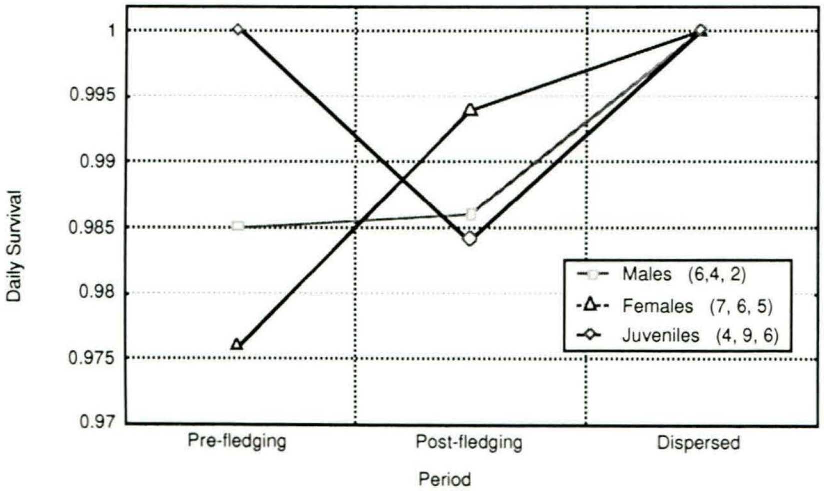

Figure 2.—*Daily survival rates for Burrowing Owls in Hanna, AB 1996. Rates are plotted separately for adult males, adult females, and juveniles across three time periods. Sample size is given in the legend for each time period (chronologically).*

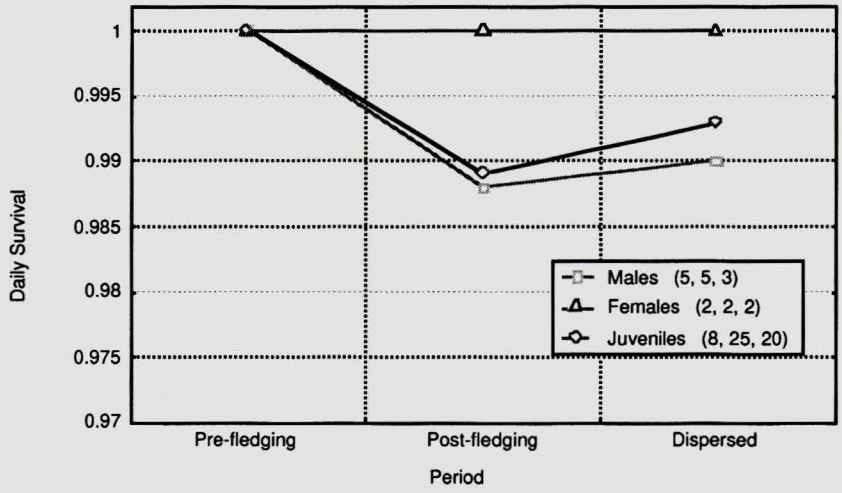

Figure 3.—*Daily survival rates for Burrowing Owls in Regina, SK 1996. Rates are plotted separately for adult males, adult females, and juveniles across three time periods. Sample size is given in the legend for each time period (chronologically).*

Table 1.—*Survival and cause-specific mortality rates for adult and juvenile Burrowing Owls from Hanna, AB and Regina, SK.*

			Cause-specific mortality			
Age/Sex	**N**	**Survival**	**Raptors**	**Mammals**	**Vehicles**	**Other**
			Hanna 1995 (30 Jun-12 Oct)			
Adult males	5	0.55	0.45	0.00	0.00	0.00
Adult females	4	1.00	0.00	0.00	0.00	0.00
Juveniles	12	0.36	0.40	0.24	0.00	0.00
			Hanna 1996 (28 Jun-21 Oct)			
Adult males	6	0.46	0.54	0.00	0.00	0.00
Adult females	8	0.48	0.31	0.00	0.00	0.21
Juveniles	9	0.60	0.13	0.27	0.00	0.00
			Regina 1996 (25 Jun-17 Oct)			
Adult males	5	0.38	0.00	0.18	0.18	0.26
Adult females	2	1.00	0.00	0.00	0.00	0.00
Juveniles	25	0.48	0.08	0.10	0.17	0.17

only incurred mortality in Hanna 1996. With the exception of males in Regina 1996, there were no adult mortalities from mammalian predators. In contrast, juveniles were killed by mammals in all three groups. Mortality from predators, both mammalian and avian, was lowest on the Regina study area. However, vehicle collisions, starvation, and miscellaneous or unidentified sources made up the balance of mortality. All mortality of adult males and juveniles in Hanna came from predators.

SUMMARY AND CONSERVATION IMPLICATIONS

Three general points of summary have emerged with some potential conservation implications.

1. Most owls were killed near the nest during the post-fledging dependency period. This is a time when the juveniles are beginning to explore flight and the adults are actively hunting to feed their still-dependent young. This peak of activity around the nest may serve as a cue to predators.

2. Despite low sample size, survival is comparable between Hanna and Regina for both adult males and juveniles. The interesting differences are in the sources of mortality. The sparsely populated and relatively 'pristine' Hanna study area had no vehicle mortalities, mostly predation. In Regina however, predators and vehicles killed about the same proportion of owls. This extensively cultivated and highly fragmented landscape probably supports lower densities of buteo hawks and canids than the Hanna region.

3. Our estimated mortality over a 5 month period, plus additional losses expected on migrations and over winter, should result in relatively low annual survival, possibly low enough to constitute a population limiting factor.

LITERATURE CITED

Einarsen, A.S. 1956. Determination of some predator species by field signs. Oregon State Monographs. 10: 1-34.

Hamerstrom, F. 1972. Birds of prey of Wisconsin. Madison, WI: Wisconsin Society for Ornithology, Department of Natural Resources.

Heisey, D.M.; Fuller, T.K. 1985. Evaluation of survival and cause-specific mortality rates using telemetry data. Journal of Wildlife Management. 49: 668-674.

Dispersal Behavior and Survival of Juvenile Tawny Owls (*Strix aluco*) During the Low Point in a Vole Cycle

C.F. Coles and S.J. Petty[1]

Abstract.—In 1996 we investigated dispersal and survival of juvenile Tawny Owls (*Strix aluco*) by radio-tracking in Kielder Forest, Northumberland, a man-made conifer forest in northern England. Here, Tawny Owls fed largely on field voles (*Microtus agrestis*) which exhibited a 3-4 year cycle of abundance, with some spatial asynchrony. Generally, vole numbers were at the low point of the cycle in 1996. Twenty-two nestlings from 11 two-chick broods were radio-tagged when 22-31 (mean 26.3) days old. Birds fledged when 29-36 (mean 32.1) days old. Eight (36.4 percent) owls died 10-106 days after fledging and before dispersing from their natal territories. Five (22.7 percent) owls died outside their natal territories 40-147 days after fledging. Five (22.7 percent) owls disappeared suddenly at 8-51 days after fledging and before the end of the dependence period, and evidence suggested that they were predated. Contact was lost with four (18.2 percent) birds 58-178 days after fledging and after they had begun to disperse. Radio-tracking data are discussed in relation to movement patterns, food resources, and habitat preferences of juvenile owls in the post fledging period.

The dispersal behavior and survival of juvenile Tawny Owls (*Strix aluco* L.) has previously been studied in a lowland broadleaved woodland at Wytham, near Oxford, England (Southern *et al.* 1954, Southern 1970, Hirons 1976). They found that Tawny Owls remained in their natal territory, and were dependent on their parents for food for 2.5-3.0 months after fledging, and before dispersing (defined as the post-fledging period; Newton 1979). Southern (1970) gave the fledging age as 32-37 days but stated that the birds usually leave the nest at 25-30 days and hide on nearby branches. Survival and dispersal have also been investigated in an upland coniferous forest. Petty and Thirgood (1989) found that in a year of poor food supply, mortality was 91.7 percent and occurred in two peaks; (i) in the period immediately following fledging, (ii) later on, but before the end of the dependence period. The initial heavy mortality was due mainly to mammalian predators, whereas later on starvation was the chief cause of death. It was also found that broods reared in a predominantly coniferous habitat showed a strong preference for roosting in broadleaved trees.

A study of first-year survival of Great Horned Owls (*Bubo virginianus*) in different phases of the snowshoe hare (*Lepus americanus*) cycle found that juvenile survival collapsed parallel to the decline in hare densities, and that mortality rates peaked before, not during, dispersal (Rohner and Hunter 1996). Nestling survival remained high in all 3 years of the study.

Our study used radio telemetry to investigate dispersal behavior and survival of juvenile Tawny Owls in Kielder Forest, northern England. Here, the Tawny Owl's chief prey, the field vole (*Microtus agrestis*), exhibits population cycles with a periodicity of 3-4 years. Breeding parameters of Tawny Owls in Kielder are highly correlated with vole abundance, where field voles constitute 78 percent of the diet by weight (Petty 1992).

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Petty (1992) showed that birds reared in the study area could take up to 4 years before being recruited into the breeding population. It was hoped that some birds would survive to become non-territorial "floaters" so that the behavior of this sector of the population could be studied in terms of our wider investigation into this hierarchical predator-prey system.

METHODS

Study Area

The study area in Kielder Forest (55°N, 2°W) was part of an extensive man-made conifer forest. It measured 480 km^2 and was planted mainly with Sitka spruce (*Picea sitchensis*) and Norway spruce (*Picea abies*) grown on 40-60 year rotations. Broadleaved trees grew along many of the watercourses and there were also some larger areas of deciduous trees, including alder (*Alnus glutinosa*) and birch (*Betula spp.*). In 1996 the forest was a mosaic of stands of different species and ages of trees. There were extensive clear-cut patches which, once colonized by grasses and rushes, provided ephemeral islands of vole habitat within the forest.

Sex Determination

Blood samples were taken from nestlings, which were sexed from female-specific minisatellite fragments (Appleby *et al.*, in press).

Age Determination

Hatch dates were estimated using a wing length/age growth curve[2]. Owls were radio-tagged before fledging, at 22-31 (mean 26.3, S.E. 0.4) days of age, and then monitored daily using telemetry. This allowed fledging ages to be calculated to within half a day. Nestlings were weighed 1-10 (mean 4.1) days before fledging and we refer to this as pre-fledging mass.

Radio Telemetry

Within the study area, most Tawny Owls bred in nest boxes which had been provided for them. Nestling owls from 11 two-chick broods were radio-tagged. These were distributed throughout the areas in which owls bred. A soft nylon harness was used to fix the transmitter to the back of the owls, leaving adequate slack to compensate for further growth (fig. 5.1B in Kenward 1987). Radio tags (Biotrack Ltd) transmitted on 173.201-173.940 MHz. The combined mass of the radio and harness was 7.3 g. This represents 1.7-2.5 percent (mean 2.1 percent) of a juvenile's mass at fledging. The radios were expected to transmit for 1 year.

A TRX 1000S receiver (Wildlife Materials Inc.) was used with a hand-held three element Yagi antenna to find the position of radio-tagged birds. Daytime roost positions were determined every 1 to 3 (mean 2) days, the frequency increasing as the bird's movements grew in magnitude. It was usual to return to the position of the previous fix to determine roughly how far the bird had moved. They were then approached until seen or until the roosting tree was located. On a few occasions triangulation was necessary in order to avoid disturbance, for example, when the birds were roosting in early-thicket spruce crops. Initially it was possible to approach birds closely, but later on they became more wary and were liable to be flushed from their perches. As a consequence, some fixes were of poorer quality than location to a specific tree, but it was always possible to identify the type and age class of forest that owls were using. Positions were plotted on a 1:10 000 scale forest stock map.

Prey Availability

Relative densities of field voles were assessed using vole sign indices (VSIs). A 25 cm^2 quadrat was thrown 25 times within a 0.5 ha patch of vole habitat nearest to the roosting position of the owls. Within these quadrats the presence or absence of fresh grass clippings in vole runs was noted. Each patch was then assigned a score on a scale of 1 to 25. The validity of this method had previously been confirmed by trapping at VSI sites and a significant relationship was found between the two indices (Petty 1992). Bank voles (*Cleithrionomys glareolus*), which occurred widely in the study area, do not produce grass clippings and therefore VSIs reflect field vole abundance.

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[2] S.J. Petty, unpublished data.

Movements and Behavior

Movements in Relation to Relative Abundance of Field Voles

Field vole abundance assessments were limited to patches near owl roosts and not performed in areas unused by owls. It was therefore not possible to analyze the data in terms of "selection" *per se*. Instead, the relative vole densities were compared for areas between which owls were moving. Analysis was conducted by using all patch to patch movements made by all owls. Each was grouped into one of three categories; (i) movement to an area of higher vole density (higher), (ii) movement to an area of similar vole density (similar), (iii) movement to an area of lower vole density (lower). Frequencies in the three categories were then compared using Chi-squared tests.

Habitat Selection

Locations of owls ($n = 319$) were compared with a random sample of tree species and age classes ($n = 351$) generated from a GIS forest stock database for the Tawny Owl study area.

RESULTS

Nestling Survival

Nestling survival was high for the 11 broods studied. Twenty-two (88 percent) of 25 young which hatched survived to fledging.

Post-fledging Survival

Juveniles fledged at 29-36 (mean 32.1, S.E. 0.6) days of age. A multiple regression was used to investigate the relationships between fledging age, pre-fledging mass, and gender. Sex and mass were significantly correlated ($p = 0.004$), but age at fledging was not related to mass ($p = 0.87$) nor sex ($p = 0.67$).

Eight (36.4 percent) owls died 10-106 days after fledging but before dispersing. That is, before they had made substantial movements outside their natal territories. Of these, five were males. A further five (22.7 percent) owls (2 males) died 40 to 147 days after fledging, having begun to disperse. Five (22.7 percent) owls disappeared suddenly at 8 to 51 days after fledging and before the end of the dependence period. Contact was lost with a further four (18.2 percent) birds at 58 to 178 days after fledging, having left their natal territories. The latter two groups were excluded from the survival and mortality analyses. The raw data is presented in table 1. On average, females lived longer than males, but this difference was not statistically significant ($t = 0.96$, d.f. = 11, $p = 0.17$).

Timing and Causes of Mortality

Peak mortality occurred at 21 to 60 days after fledging with a lower, fairly even distribution from 61 to 120 days (fig. 1). Three owls were predated by Northern Goshawks (*Accipiter gentilis*) early on (before 41 days) whereas starvation, which accounted for six deaths, occurred more evenly throughout the study period at between 10 and 93 days after fledging (table 1). No more deaths from starvation occurred after the end of the dependence period (75-90 days). An owl was found dead with a field vole lodged in its throat 73 days after fledging, but with no other signs of injury or disease. One bird was found buried, decapitated and wingless after 106 days, and another, found 147 days after fledging, had half its skull missing and a broken wing. In both cases the bird's pectoral muscle mass was relatively high and starvation was unlikely, and there were no other obvious signs of the cause of death. The injuries were likely to have been sustained *post mortem*, possibly as a result of scavenging by a red fox (*Vulpes vulpes*) and a weasel (*Mustela nivalis*) respectively. Finally, a juvenile female, found dying in a ditch 106 days after fledging, had suffered an eye injury but otherwise seemed to have been in fair condition.

Relationship Between Days Lived After Fledging and Fledging Date

For the 13 birds whose fate was known there was a highly significant negative correlation between their fledging date in June and the number of days lived prior to fledging ($F = 23.25$, $p < 0.01$). That is, birds which fledged earlier tended to live longer (fig. 2). A multiple regression was performed to investigate the effects of the possible confounding influences of sex and weight (close to fledging date). Only fledging date had a significant relationship with survival and accounted for 68 percent of the variation ($F = 23.25$, $r^2 = 67.88$, $p < 0.01$). Survival was not significantly correlated with pre-fledging mass ($p = 0.17$) nor sex ($p = 0.13$), but mass was significantly correlated with sex

Table 1.—*Survival, mortality and movements of 22 radio-tagged juvenile Tawny Owls in Kielder Forest, northern England. The forth column shows the number of days after fledging until death or loss of contact for each bird. Displacement represents distance moved in a straight line drawn from nest boxes to the position of the last fix.*

Identity	Sex	Fate	Dead/missing @ (days)	Cause of death	Displacement (km)	Started to disperse?
GF36858	f	dead	80	starvation	0.39	n
GF36857	m	dead	39	starvation	0.04	n
GF36861	m	dead	147	?	3.04	y
GF36890	f	dead	106	eye injury	0.79	n
GF36883	f	dead	106	?	3.98	y
GF36884	m	missing	33			n
GF36900	f	dead	47	goshawk	2.17	y
GF36875	m	missing	61		2.85	y
GF36898	f	dead	27	starvation	0.11	n
GF36899	m	dead	54	starvation	1.6	y
GF36894	m	missing	51		0.9	n
GF36893	f	missing	50		0.95	n
GF36892	m	dead	22	goshawk	0.25	n
GF62107	m	dead	10	starvation	0.91	n
GF36859	m	missing	178		0.76	y
GF36860	m	missing	88		0.12	y
GF36881	f	dead	93	starvation	0.87	y
GF36882	m	dead	73	not starvation but ?	0.36	n
GF36867	m	dead	47	goshawk	0.65	n
GF36868	f	missing	40		0.65	n
GF36869	m	missing	8			n
GF36870	f	missing	58		1.03	y

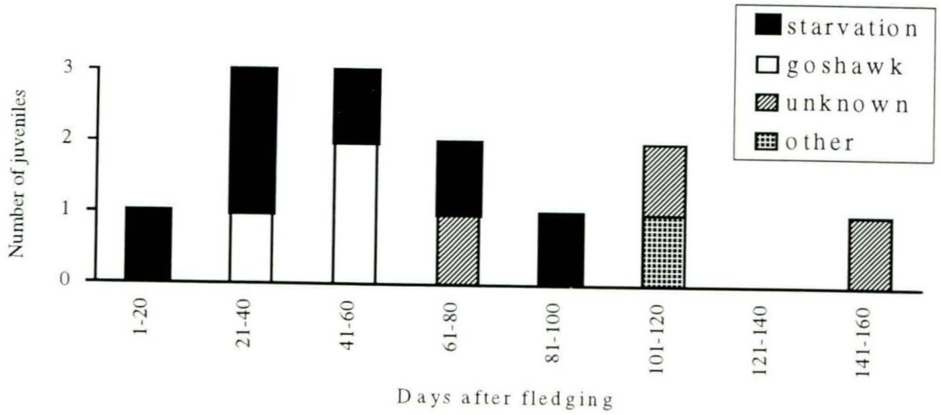

Figure 1.—*Timing and causes of mortality for 13 juvenile Tawny Owls in Kielder Forest, northern England. The dependence period ends at approximately 75-90 days.*

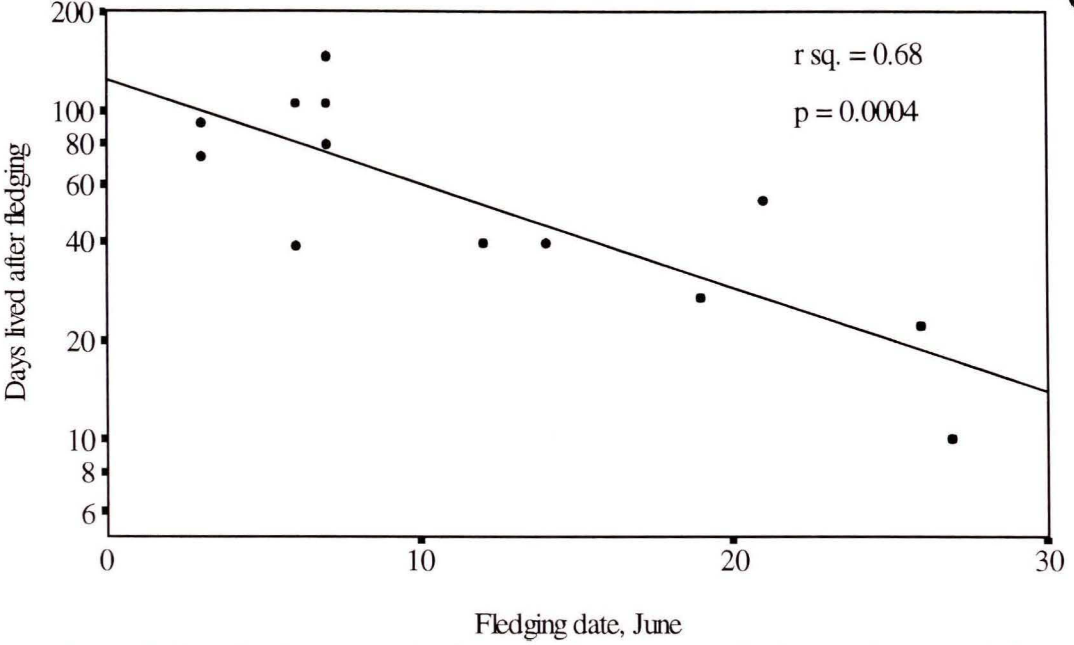

Figure 2.—*Relationship between the fledging date of juvenile Tawny Owls and the number of days lived after fledging in Kielder Forest, northern England. The points represent the 13 owls which were known to have died.*

(p = 0.02), as one might expect given that female Tawny Owls are larger than males (Petty 1992, p. 8).

Prey Availability

In 1996, vole numbers were generally low, although there were "hotspots" of higher vole densities to which owls largely confined their breeding attempts. Thus, dispersing owls were presented with an extremely patchy food supply. The highest vole density at any one site in 1996 was 150/ha and the lowest was 0/ha. Recapture analysis indicated a 95 percent chance of catching whatever animals were present. Average densities for Kielder in 1996 were: (i) spring 46/ha, (ii) summer 54/ha, and (iii) autumn 35/ha (J.L. Mackinnon, unpubl. data).

Movements and Behavior

Movements of owls between roosting sites were measured as linear distances between fixes. It became apparent that movements of owls between roosting sites over a period of time were seldom unidirectional. Individual birds made "to and fro" movements between favored stands of trees, sometimes leaving the natal territory, only to return later. There were also large scale circular movements, often with over 1 km between stages.

Birds with which contact had been lost had moved between 0.12 and 2.85 km (mean 0.88 km) before they "disappeared".

For the birds which were found dead, movement distances, defined as linear distance between the natal nest box and the position of the last fix, ranged from 0.02 to 3.98 km (mean 1.10 km). This underestimated total distance covered by dispersing owls, because to and fro and circular movements, and forays were not taken into account. Two owls moved suddenly from their natal territories well before the end of the dependence period and subsequently died. Of these, one starved 1.60 km from its nest box, and the other was predated by a goshawk 2.17 km from its nest site (table 1). Eight owls remained within their natal territories, moving 0.02 to 0.79 km (mean 0.33 km) from their nest boxes before dying. Five owls moved outside their natal territories, moving 0.87 to 3.98 km from their nest boxes in gradual, stepped movements of up to 1.2 km. The behavior of two of these, plus another where contact was subsequently lost, is described in detail below.

Movements in Relation to Relative Abundance of Field Voles

For this preliminary analysis, expected values were calculated assuming that birds had a free choice of the three patch types each time they

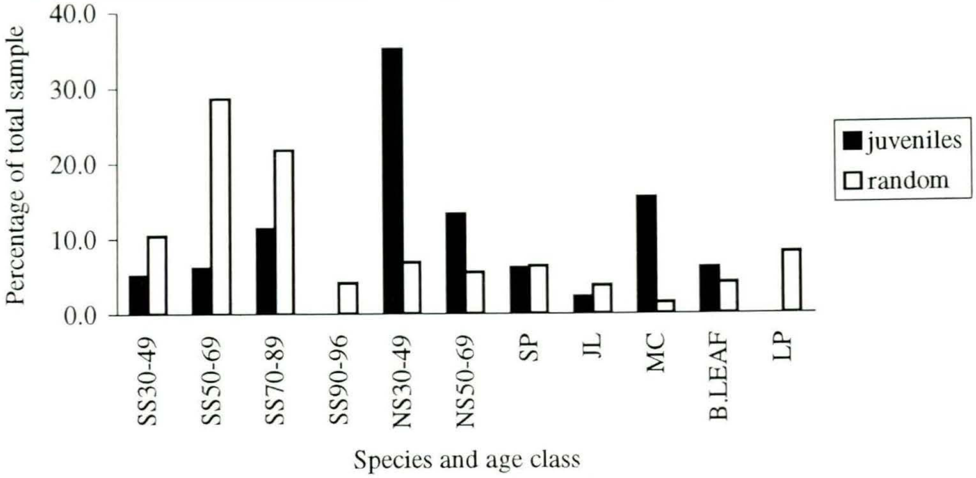

Figure 3.—*Comparison of habitats used by juvenile Tawny Owls for roosting with a random sample of similar size from a GIS database of the Kielder Forest, northern England Tawny Owl study area. Numbers on the X axis represent planting years, and the species are coded as follows: SS = Sitka spruce, NS = Norway spruce, JL = Japanese larch, MC = mixed conifers, B.LEAF = broadleaved trees, LP = Lodgepole pine.*

moved. In reality this may not have been the case. Overall, the frequencies in these groups were significantly different ($\chi^2 = 7.92$, d.f. = 2, $p < 0.05$, $n = 32$). Chi squared tests were calculated for each group of values. There were significantly fewer movements to similar areas ($\chi^2 = 4.2$, d.f. = 1, $p < 0.05$) and roughly equal numbers of movements to lower areas than would be expected by chance ($\chi^2 = 0.008$, d.f. = 1, $p > 0.05$). There were more movements to higher areas than expected by chance but this result was not statistically significant ($\chi^2 = 3.7$, d.f. = 1, $p > 0.05$).

The behavior of three longer-lived juveniles differed in two areas with widely different average vole abundance scores. In area 1, with an average VSI score of 1.7, GF36861 made circular and reciprocal movements between six patches of vole habitat, rarely stopping at each one for more than 2-3 days. This bird continued to move widely until it was found dead. By contrast, in area 2, where the average VSI score was 7.7, GF36859[3] and GF36881 roosted in a stand of trees between two large clear-felled patches for 80 and 21 days respectively, after previously having made extensive movements between patches of lower vole densities.

Habitat Selection

Overall, there were highly significant differences between the habitat where owls chose to roost and that which was available to them ($\chi^2 = 882$, d.f. = 10, $p < 0.01$).

Owls used older stands of Sitka spruce ($\chi^2 = 65$, d.f. = 1, $p < 0.01$) less than expected by chance. Older stands of Norway spruce ($\chi^2 = 323$, d.f. = 1, $p < 0.01$), and stands of mixed coniferous crops ($\chi^2 = 387$, d.f. = 1, $p < 0.01$) were used more than would have been expected by chance. Proportions of Scots pine (*Pinus sylvestris*), Japanese larch (*Larix kaempferi*), and broadleaved species used by owls were similar to their availability (fig. 3). Lodgepole pine was represented in the forest but grows at higher elevations on blanket peat bogs and was therefore unused by the owls. This preliminary analysis does not take altitudinal and planting patterns into account, and does not necessarily represent the habitat available to owls in specific territories.

DISCUSSION

Like Rohner and Hunter (1996), we found high nestling survival even though owls were under food stress.

We were able to confirm previous estimates of the age at which chicks fledged (Southern 1970) and show that one calendar month is a fair approximation.

It was expected that heavier nestlings would fledge earlier than lighter nestlings, but we found no relationship between age and pre-fledging mass, nor between fledging age and gender. Tawny Owls are sexually dimorphic (mass = 1.3:1 female:male, Petty 1992) which accounted for the significant relationship between sex and mass. A possible problem with this analysis was variation in the period of time which elapsed between the last weighing and fledging, although there were relatively few birds which were last weighed more than 5 days before fledging.

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[3] This bird subsequently disappeared from the area and contact was lost.

Survival rates of Tawny Owls in spruce forests were much lower in decreasing vole years (Petty 1992). In Kielder Forest in 1996, juvenile mortality was extremely high, with a large proportion of birds starving. A trend toward greater longevity in females may simply be a function of the analysis, in that missing birds were excluded and these included some relatively old males (table 1).

Unlike Petty and Thirgood (1989), our study found that owls starved throughout the post-fledging period, rather than just before the on-set of independence. This could be a function of low vole densities in Kielder in 1996, as opposed to densities which were declining from a higher level in Glenbranter, Argyll in 1986 (Petty and Thirgood 1989). However, there was agreement between the two studies in that predation was an important factor early in the dependence period, although predators responsible differed between the two studies. Younger owls may be less able to evade predators before their flight feathers are fully developed, and this may have been exacerbated by an interaction between food shortage and predation, where owls in poor condition seem to be more vulnerable (Rohner and Hunter 1996). For example, one bird could be approached to within a few meters before it flew to a safer perch. It was subsequently killed by a goshawk. Hungry juveniles also call more and their parents are less aggressive towards potential predators.

The period for which our juveniles survived after fledging was strongly correlated with their fledging date. Petty (1992) showed that hatch-date (a surrogate for fledging date) had a strong influence on future recruitment in declining vole years, but not in low or increasing vole years. Thus, in declining vole years, a greater proportion of early-hatched chicks survived to breed. In most previous low vole years, vole numbers increased towards the autumn so that owls entered the winter with a good food supply. However, 1996 was different because vole numbers did not recover later on in the year. This may account for the particularly heavy mortality that we observed.

For the five owls which disappeared suddenly, there was no evidence of transmitter failure prior to loss of contact—similar tags on adult owls remained functional throughout this study. The birds may have been predated but it is also possible that the tags had been damaged or buried by predators, such as foxes, or lay in "dead ground" such as a ditch, stream or hollow, where the signal range would have been reduced. Goshawks pluck avian prey and may remove the carcass, so piles of feathers without a radio transmitter could have been overlooked. Indeed, on one occasion a goshawk was disturbed and a decline in signal strength was heard as the predator removed the carcass. Of the four owls where contact was lost after 58 days, all except one had made wide-ranging movements prior to their disappearance. Although predation or tag failure could not be ruled out, it is possible that these birds had suddenly dispersed.

It was evident from this study that telemetry can provide valuable information on movement and behavioral patterns during dispersal that cannot be gathered in any other way. In particular, the relationship between owl movements and their food supply was tentatively illustrated. The contrasting behavior of owls in two areas of widely different food availability was a particularly noteworthy result, although the sample size was small.

Paton *et al.* (1991) showed that backpack-mounted radio tags had adverse effects on the survival of Spotted Owls (*Strix occidentalis*), although few deaths could be directly attributed to the radio tag or harness. Also, radios represented 2.8-4.1 percent of their owl's mass which was on average rather more than the burden that our birds carried. Future work will use tags and harnesses of the same design as those used in 1996, so that any effects can be quantified and standardized between years.

Unlike Glenbranter in 1986 (Petty and Thirgood 1989), in Kielder there was no evidence that juveniles showed a strong preference for roosting in broadleaved as opposed to coniferous trees. However, there are fewer broadleaves in Kielder than Glenbranter. In general, the forest structure in Kielder seemed important with birds preferring to roost in taller, more widely spaced stands, and avoiding more dense stands (personal observation). Our use/availability analysis took the study area as a whole, and was not necessarily an accurate representation of the habitat available to owls in individual territories. Further analysis is required.

Due to the very high rates of mortality observed in this study it may be concluded that none or few of the 1996 cohort will have survived to become recruits or "floaters". If there are non-territorial owls in Kielder, then it is likely they were hatched in years when vole densities were higher. We will repeat this work in 1997 when vole numbers should be increasing.

ACKNOWLEDGEMENTS

We are grateful to the Forestry Commission staff in Kielder Forest District for their co-operation and to the British Trust for Ornithology for providing the licences that were required. Dr. Bridget Appleby took and analyzed blood samples to provide sexes for nestlings. Mr. James MacKinnon generously allowed us to use his unpublished data. Dr. Chris Thomas extracted data from a GIS database and kindly commented on an earlier draft of this paper, as did Drs. Steve Redpath and Tom Sherratt. The research was conducted with funding from a studentship as part of a NERC Large Scale Processes in Ecology and Hydrology Special Topic, grant GST/02/1218.

LITERATURE CITED

Appleby, B.M.; Petty, S.J.; Blakey, J.K.; Rainey, P.; Macdonald, D.W. 1997. Does variation of sex ratio enhance reproductive success of offspring in tawny owls *Strix aluco*. Proceedings: Biological Sciences. [In press.]

Hirons, G.J.M. 1976. A population study of the Tawny Owl *Strix aluco* L. and its main prey species in woodland. University of Oxford. Ph.D. dissertation.

Kenward, R. 1987. Wildlife radio tagging. London: Academic Press. 222 p.

Newton, I. 1979. Population ecology of raptors. Berkhamsted: T & A.D. Poyser. 399 p.

Paton, P.W.C.; Zabel, C.J.; Neal, J.L.; Steger, G.N.; Tilghman, N.G.; Noon, B.R. 1991. Effects of radio tags on spotted owls. Journal of Wildlife Management. 55: 617-622.

Petty, S.J. 1992. Ecology of the Tawny Owl (*Strix aluco*) in the spruce forests of Northumberland and Argyll. Open University. 295 p. Ph.D. dissertation.

Petty, S.J.; Thirgood, S.J. 1989. A radio tracking study of post-fledging mortality and movements of Tawny Owls in Argyll. Ringing and Migration. 10: 75-82.

Rohner, C.; Hunter, D.B. 1996. First-year survival of Great Horned Owls during a peak and decline of the snowshoe hare cycle. Canadian Journal of Zoology. 74: 1092-1097.

Southern, H.N. 1970. The natural control of a population of Tawny Owls (*Strix aluco*). Journal of Zoology. 162: 197-285.

Southern, H.N.; Vaughan, R.; Muir, R.C. 1954. The behaviour of young Tawny Owls after fledging. Bird Study. 1: 101-110.

Seasonal Distribution of the Great Gray Owl (*Strix nebulosa*) in Southwestern Alberta

Douglas M. Collister[1]

Abstract.—Great Gray Owls (*Strix nebulosa*) have been banded and monitored west of Calgary in the foothills of Alberta from 1986 to 1996. Thirty-six adult owls have been banded: 16 males, 16 females and 4 of unknown sex. Great Gray Owls were captured during every month except August and October although the majority (56 percent) were banded from March-May (n=18). Four birds have been recaptured to date. A male was caught in the same location on 23 March and 9 May of 1986, a female was caught in the same location on 31 May 1987 and 18 November 1989, a female banded on 26 December 1988 was road-killed 14 km SSE on 19 September 1992, and a male banded on 17 June 1989 was recaptured 15 km NNE on 20 May 1990. Evidence of winter (non-breeding) territoriality has been observed. Seasonal change in abundance, indicative of a significant movement of birds into or out of the study area, has not been observed. Due to sub-regional variations in topography and climate, the study area encompasses a wide range of habitat types including muskeg, mature upland poplar-spruce mixed forest, old-growth riparian spruce forest and grasslands. The diversity inherent in this landscape appears to satisfy year-round habitat requirements for the Great Gray Owl, precluding a requirement for this species to exhibit large-scale seasonal migratory movements.

The Great Gray Owl (*Strix nebulosa*) breeds in northern and western Alberta south to Waterton Lakes National Park (Semenchuk 1992). In south-western Alberta the species is associated with mature coniferous and mixed forests. The Great Gray Owl exhibits irregular southward, often spectacular, invasions in many areas of its range. These irruptions are thought to be related to prey availability (Mikkola 1983, Nero 1980). Non-irruptive long-distance movements have also been documented. In Oregon, birds may move seasonally up to 43 km while in Manitoba individuals may migrate up to 700 km (Bull and Duncan 1993). In recent years major irruptions of Great Gray Owls in eastern North America occurred in 1978-1979, 1983-1984, and 1991-1992 (Bull and Duncan 1993).

Irruptions of Great Gray Owls do not appear to occur in southwestern Alberta. This area appears to harbor a breeding population that is more or less observable dependent on winter snow thickness and prey density (pers. observ.). In this paper I offer data and provide a possible explanation why this is so.

STUDY AREA

The study area is a 55 km long by 32 km wide area along the Rocky Mountain Foothills, northwest of Calgary, from approximately latitude 51°10′N to 51°45′N and longitude 114°30′W to 115°00′N. Five natural subregions representing four of Alberta's Natural Regions occur in the study area (AEP 1994). Vegetational, climatic and elevational characteristics of these natural subregions results in a varied sub-regional landscape (table 1).

BANDING

Great Gray Owls have been banded, opportunistically, in the study area since 1986. A total of 36 adult owls have been marked through 31 December 1996 including 16 males, 16 females, and 4 of unknown sex. Owls were captured using a landing net or a bal-chatri baited with a dark-colored laboratory mouse as

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Table 1.—*Characteristics of natural regions and subregions comprising Great Gray Owl habitat in southwestern Alberta.*

Natural region	Natural subregion	Vegetation	Miscellaneous
Parkland	Foothills Parkland	aspen groves, closed aspen and poplar forest, grassland, willow groveland	≤ 1300 m elevation
Foothills	Lower Foothills	mixed forests of white spruce, black spruce, lodgepole pine, balsam fir, aspen, white birch and balsam poplar	winters are moderated by chinook winds
Foothills	Upper Foothills	forests dominated by lodgepole pine, white spruce, black spruce, and sub-alpine fir	greatest summer precipitation in Alberta (340 mm)
Rocky Mountain	Montane	forests of Douglas-fir and limber pine, lodgepole pine, white spruce, and aspen, grasslands	characterized by landscape pattern of open forests and grasslands, "chinook" winds cause intermittent snow-free conditions
Boreal Forest	Dry Mixed	mixed forests of aspen, poplar, white spruce, balsam poplar, and jack pine, peatlands	

a lure. Birds were banded or recaptured during every month of the year except August and October. The number of adults captured was spread evenly throughout the year, with a slight increase during May when adults are feeding nestlings; Jan (3), Feb (2), Mar (5), Apr (5), May (10), Jun (5), Jul (3), Sep (3), Nov (1), Dec (4).

Four re-encounters with banded Great Gray Owls have provided insight into their seasonal movement and distribution. A male banded on 23 March 1986 approximately 4 km southwest of Water Valley was recaptured there on 9 May. No nest was found but this bird was possibly on a breeding territory. A female was banded on 31 May 1987, also approximately 4 km southwest of Water Valley, and recaptured within 800 m of that site on 18 November 1989. This bird possibly maintained a home range during the breeding and non-breeding seasons. A female banded on 26 December 1988 approximately 15 km southwest of Bergen was found dead on a road on 19 September 1992 approximately 6 km west of Water Valley. This bird was 14 km to the south-southeast after 4 years. A male, banded on 17 June 1989 approximately 4 km southwest of Water Valley, was recaptured on 20 May 1990 approximately 12 km north-northwest of Water Valley. This bird was 15 km to the north-northeast.

CHRISTMAS BIRD COUNTS

The Cochrane Wildlife Reserve Audubon Society Christmas Bird Count (CBC), positioned within the study area (center 51°26′N, 114°35′W), has been compiled since 1974 (23 years). Observations of Great Gray Owls from this CBC was normalized to calculate owls observed per 10 observers (fig. 1). Number of observers provides the best average correlation and the most frequent highest correlation with CBC data (Raynor 1975). The resultant bar graph shows an increasing cyclical pattern within what may be a natural range of variation. There is little suggestion of an irruption during any of the years presented.

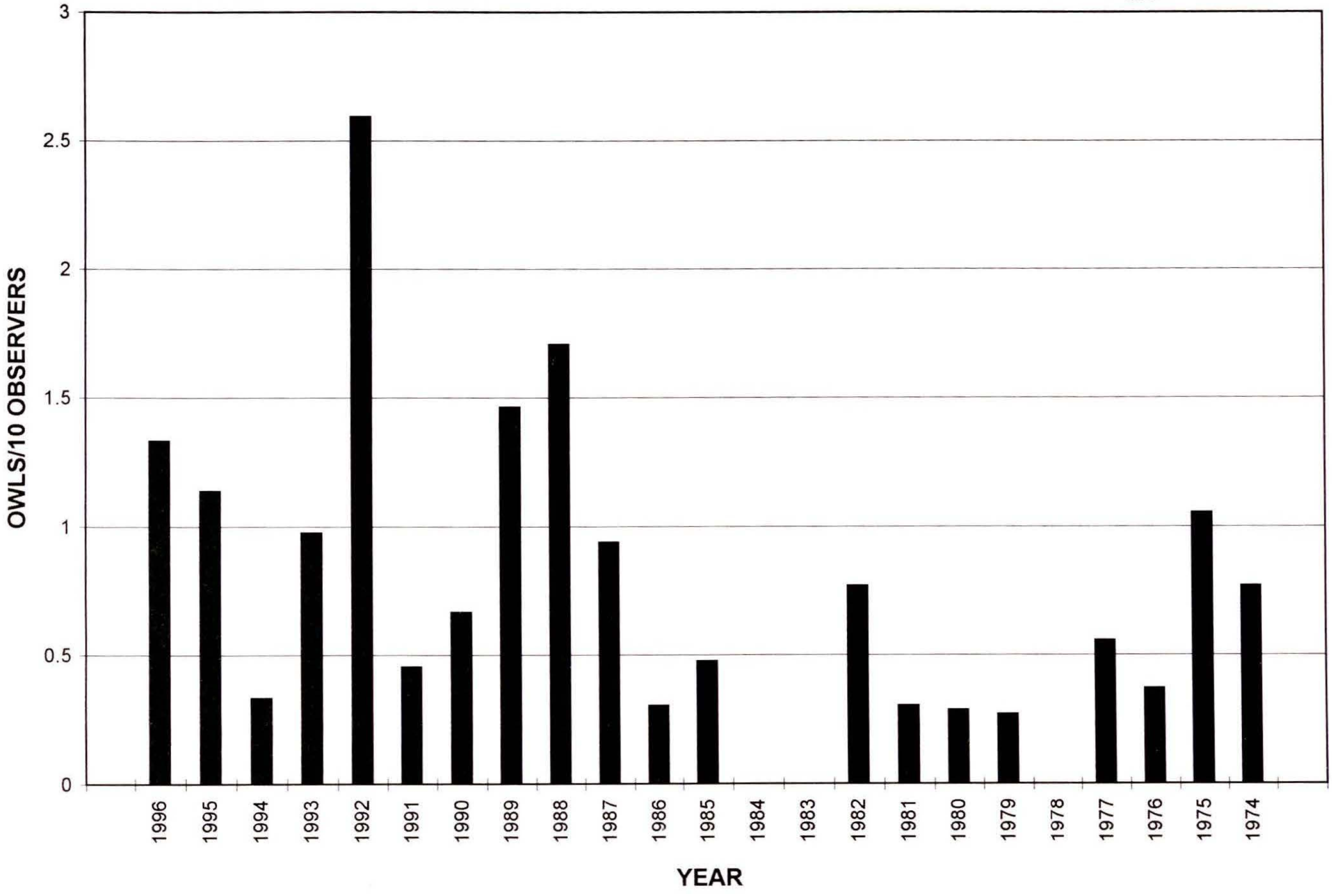

Figure 1.—*Great Gray Owl occurrence on the Cochrane Wildlife Reserve based on Audubon Christmas Bird Count in southwestern Alberta, 1974-1996.*

WINTER (NON-BREEDING) TERRITORIALITY

Intraspecific aggression, perhaps winter territoriality, has been observed in Ontario and Manitoba (Brunton and Pittiway 1971, Nero 1980). Although territoriality in this species requires further study (Bull and Duncan 1993), owls that do not disperse seasonally may be territorial much of the year. One incident of non-breeding intraspecific aggression, possibly territoriality, has been observed in the study area. The species is not known to defend foraging areas during the breeding season (Bull and Duncan 1993). On 26 November 1993 a Great Gray Owl was observed to fly from its hunting perch towards another Great Gray Owl hunting approximately 100 m away. The second bird retreated 150 m or so to the forest edge while the aggressor returned to its original perch where it vocalized several times.

LANDSCAPE CONSIDERATIONS

Five natural subregions representing four of Alberta's natural regions comprise the study area (AEP 1994) (table 1). Forests range from pure aspen to mixed to lodgepole pine and spruce. Petroleum exploration, forestry, and agriculture are all active industries in the Rocky Mountain Foothills and are contributing to a progressively more fragmented landscape. Great Gray Owls benefit from early stages of forest fragmentation (Bull and Duncan 1993). As a result, juxtaposition of forest, suitable for nest sites, with grasslands and openings is more frequent. Elevation in the study area can change locally 100 to 200 m in less than a kilometer. The resultant aspect and slope variation contributes to an exceptionally heterogeneous landscape.

DISCUSSION AND SUMMARY

Dramatic fluctuations of Great Gray Owl numbers in southwestern Alberta that would suggest irruptive movements were not observed in the study area. Owls were observed and captured for banding in all seasons. Recoveries of banded birds suggest that Great Gray Owls remain in the study area year-round, perhaps within a kilometer or two. Christmas Bird Count data does not suggest an irruption since 1974.

Due to its inherent landscape heterogeneity and land-use modification, the study area offers Great Gray Owls a wide selection of habitat alternatives in close proximity. Other studies in areas of topographic relief have indicated elevational rather than spatial adjustments by owls between seasons. Franklin (1987) found wintering Great Gray Owls at lower elevations than during the breeding season. It seems likely that prey availability and other ecological factors in southwestern Alberta vary widely across short distances such that long-range movement by Great Gray Owls to satisfy seasonal requirements is unnecessary.

ACKNOWLEDGMENTS

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LITERATURE CITED

Alberta Environmental Protection. 1994. Natural regions and subregions of Alberta: summary. Publ. I/531. Edmonton, AB: Alberta Environmental Protection. 18 p.

Brunton, D.F.; Pittaway, R., Jr. 1971. Observations of the Great Gray Owl on winter range. Canadian Field-Naturalist. 85: 315-322.

Bull, E.L.; Duncan, J.R. 1993. Great Gray Owl (*Strix nebulosa*). In: Poole, A.; Gill, F., eds. The birds of North America. No. 41 Philadelphia, PA: The Academy of Natural Sciences; Washington, DC: The American Ornithologists' Union.

Franklin, A.B. 1987. Breeding biology of the Great Gray Owl in southeastern Idaho and northwestern Wyoming. Arcata, CA: Humboldt State University. M.S. thesis.

Mikkola, H. 1983. Owls of Europe. Vermilion, SD: Buteo Books. 397 p.

Nero, R.W. 1980. The Great Gray Owl-phantom of the northern forest. Washington, DC: Smithsonian Institution Press. 167 p.

Raynor, G.S. 1975. Techniques for evaluating and analyzing Christmas bird count data. American Birds. 29(2): 626-633.

Semenchuk, G.P. 1992. The atlas of breeding birds in Alberta. Edmonton, AB: Federation of Alberta Naturalists. 390 p.

Burrowing Owl (*Speotyto cunicularia*) Monitoring and Management Activities in Manitoba, 1987-1996

Ken D. De Smet[1]

Abstract.—Monitoring of Burrowing Owl (*Speotyto cunicularia*) populations in Manitoba from 1987-1996 revealed a continuous population decline from 34 known nesting pairs to only one. Management activities are discussed including public awareness programs, reintroductions, habitat protection and provision of artificial nest burrows. Nest reuse in consecutive years ranged from 7 percent for 57 failed nests to 23 percent for 122 successful nests. Only 14 percent of unsuccessful territories were reused compared to 51 percent of successful sites. Higher nest reoccupancy rates were noted for artificial burrows (44 percent; n=27) than for natural nests (13 percent; n=152). Low return rates of banded juveniles (3.5 percent; n=538) and adults (32.7 percent; n=165) suggest that reduced survivorship may be a contributing factor to observed declines. Adult males returned more frequently (40.2 percent) than females (24.4 percent). Males were more frequently re-encountered at the same nest (51 percent) or within 1 km (94 percent) than females (33 percent and 56 percent, respectively). Average dispersal distances between years were 3.0 km for adult males (n=35) and 10.9 km for adult females (n=18). Average dispersal distances for juveniles ranged from 1-77 km, averaging 29.5 km for 9 males and 33.7 km for 9 females. Average brood size (5.1 yg/pr) and overall productivity (3.4 yg/nesting pr) appeared adequate for population maintenance.

BACKGROUND

Wildlife that inhabit North America's plains have suffered greater losses since settlement than any other group. Some prairie species have been extirpated throughout much of their range. Others like the Burrowing Owl are rapidly disappearing. This article will: (1) summarize Burrowing Owl monitoring and management efforts in Manitoba from 1987-1996; and (2) relate observed population trends to reproductive success and return rates.

Historic records of Burrowing Owl (*Speotyto cunicularia*) numbers and distribution in Manitoba are limited. The species was probably always present in extreme southwestern Manitoba. Although it was not listed in Seton's (1890) "Birds of Manitoba", this publication overlooked a number of other uncommon birds for south-western Manitoba, including the Ferruginous Hawk (*Buteo regalis*), Rough-winged Swallow (*Stelgidopteryix semipennis*), Say's Phoebe (*Sayornis saya*), Indigo Bunting (*Passerina cyanea*), Lark Bunting (*Calamospiga melanocorys*), Mountain Bluebird (*Sialia currucoides*), Lark Sparrow (*Chondestes grammacus*), Grasshopper Sparrow (*Ammodramus sanannarum*), and Nelson's Sharp-tailed Sparrow (*Ammodramus nelsoni*) (all listed as specialties in the Birder's Guide to south-western Manitoba (Cuthbert *et al.* 1990)). Some of these oversights were corrected in later publications (Seton 1893, 1908), but a shortage of observers from the extreme southwest resulted in minimal information for this region. As was the case with many of the southwestern specialties, initial Burrowing Owl reports were from south-central Manitoba (two specimens were taken near Portage la Prairie in 1897 and two more in 1899 (Seton 1908)). Indications of declines started in the late 1920's, when they were observed "becoming scarce" north of Winnipeg

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(Lawrence 1927). By the mid-1930's, the species "had greatly increased in numbers in its original stronghold in the southwest corner of the province" and it had reached its eastern limits just east of Winnipeg and north to Dauphin (Lawrence 1937). Ongoing declines since then have been attributed to habitat loss and degradation brought on by modern agricultural practices, larger farms, fields and machinery, and elimination of fence lines and waste areas (Wellicome and Haug 1995).

A mid-1970's Canadian status report prepared by Wedgwood (1978) gave an estimate of 110 nesting pairs for Manitoba. This educated guess undoubtedly under-estimated the actual population size at this time, which may have exceeded 500 nesting pairs. Limited surveys, begun in 1982 and based primarily on widespread public awareness and follow-up of reports, revealed a known population of 76 pairs (Ratcliff 1987). This number was probably still several times lower than the actual total—even with more widespread and intensive surveys, increased public awareness, audio-playback, and better knowledge on how and where to look for owls, totals during the late 1980's and 1990's were still believed to account for less than half of the actual nesting pairs (De Smet 1992a). Similar surveys in 1983 and 1984 revealed a decline to 35 known pairs and a significant range reduction (Ratcliff 1987). Thomson (1988) conducted limited monitoring in 1986 and installed 32 wooden artificial nest burrows (ANBs) in seven occupied pastures. He also prepared a provincial recovery plan which called for continued monitoring, reduced use of certain insecticides, mitigation of burrows lost to cultivation, reintroductions to supplement declining wild populations, protection of nesting sites, and more widespread public awareness and involvement.

1987-1996 SUMMARIES

Work on the present study began in 1987, when conservation efforts for Burrowing Owls and other rare, threatened and endangered grassland birds in Manitoba were integrated. Somewhat diluted Burrowing Owl surveys revealed 14 nesting pairs, 6 singles and many unsubstantiated reports (De Smet, unpubl. data). Reintroductions were started near Oak Hammock Marsh (north of Winnipeg); 16 young and 2 adults from the Owl Research and Rehabilitation Foundation (Ontario) and from roadsides near Regina (Saskatchewan) were held in preconstructed pens for 1 week, released and subsequently fed on a daily basis until natural food remains were found in the pellets (Hiltz 1987). Some critical nesting areas for Burrowing Owls and other threatened grassland species were afforded protection from cultivation and spraying via paid or voluntary 5- to 10-year leases between landowners and the Manitoba Habitat Heritage Corporation.

In 1988, two field crews conducted threatened grassland bird and Burrowing Owl monitoring and management activities. Burrowing Owl surveys were more intensive, but focused on historic nesting areas. An audio-playback technique was employed to assist in locating territorial Burrowing Owls (Haug and Didiuk 1993). Increased search effort and improved techniques resulted in 28 pairs and 6 singles being found (Haug and Churchward 1989). Releases at Oak Hammock were continued (10 yg from Ontario) and a separate release was conducted near Lyleton in extreme southwestern Manitoba (29 yg/ads from Saskatchewan).

More widespread and intensive surveys in 1989 included following up reports, checking historic areas and scanning suitable-looking sites using audio-playback (De Smet and Conrad 1989). Suitable, but previously unoccupied, sites accounted for almost half of the pairs located during this and later years, thus demonstrating the importance of combining scans of previously unoccupied pastures with surveys in historic or traditional sites. Public awareness included a mail-out of a brochure and insecticide alert, newspaper articles, year-end reports and summaries, posters, several TV and radio appearances, involvement of local interest groups and landowners, information booths, displays, tours and public presentations. Enhanced public awareness and search effort resulted in 34 pairs being found. Monitoring of reproductive success and banding efforts were also increased; a total of 109 young and 31 adults were banded with aluminum and colored plastic leg bands (these numbered bands permitted identification of returning owls without having to recapture them). To increase reporting rates on migration and the wintering areas, selected primaries of some of the young were color-marked. Notices were placed in major ornithological journals and were sent to biologists and birdwatchers throughout western North America. Totals of

23 young and 5 adults from Saskatchewan were released near Broomhill in southwest Manitoba. Wooden ANBs from 1986 were cleaned out; many had rotted and were replaced with plastic ANBs consisting of 6-inch drainage tile piping leading into a plastic pail with a short post near the entrance for perching.

Poor spring survey conditions in 1990 resulted in reduced surveys and a 44 percent reduction to 19 nesting pairs (De Smet 1991). Expanded releases included 48 yg and 4 adults from roadsides or partial families from larger broods in Saskatchewan. Eleven adults and 93 young were banded and most nesting adults were checked on an annual basis to assess banding status and return rates. Limited color-marking and widespread publicity was also employed, but this was discontinued due to few winter or migration reports (one color-marked young recovered alive in November on an oil derrick barge 20 miles off the south coast of Louisiana in the Gulf of Mexico represents the only winter or migrant report from 538 young and 94 adults from natural nests and 261 released yg/ads that were banded during this study).

In 1991 two university students began grassland bird studies in southwestern Manitoba (Davis 1994, Hellman 1994). A slight increase in nesting Burrowing Owl populations was attributed to ideal spring survey conditions (De Smet 1992a). The 23 nesting pairs included a released juvenile male from 1990. A monitoring and release program was initiated in prairie dog colonies in southwestern North Dakota. Sufficient numbers of pairs and young were located to justify relocating 50 young (partial families from larger broods) to Broomhill (De Smet *et al.* 1992). A special effort was made to contact all landowner and municipalities to notify them about nesting owls and thus lessen the chances of nest failures due to use of hazardous insecticides.

In 1992, a Natural Resources office was set up in southwest Manitoba (Melita) to facilitate endangered grassland bird management, awareness and public participation. Encouraging signs included 27 nesting pairs, five small "colonies", and a pair nesting in a 1989 ANB for the second consecutive year (De Smet 1992b). But, lowered productivity was noted due to cool, wet weather patterns that reduced food supplies (pairs were observed hunting for extended periods in sites where grasshoppers were normally abundant) and several nests were lost to badgers, including all four nests in one colony. Although adequate burrows were available, 40 additional ANBs were provided near active nests, in suitable pastures or at historic sites to lessen depredation losses. A new release technique was employed involving 16 one-year-old Burrowing Owls from Ontario; immediate success was observed as five pairs nested and one raised four young.

A slight population decline to 23 pairs was observed in 1993 despite extended mid-summer surveys (De Smet 1993). Incessant rainy, cool mid-summer weather resulted in low nesting success (30 percent) and reduced brood sizes ($\bar{X}$=3.1). Several pairs deserted clutches during late incubation and many young starved. Ultimately, less than one young was produced per nesting pair. Two separate releases were conducted with 26 one-year-olds from Ontario and the Alberta Birds of Prey Centre. Again, five nesting pairs were formed, including two wild-release pairings, but bad weather contributed to all failing. The only good news was that four wild pairs selected ANBs. To take advantage of the additional protection afforded to eggs, young and adults in ANBs, most of the other wild pairs were relocated from natural nests to ANBs using a technique originally employed in Idaho (Olenick 1990). Although nests were usually replaced during pre-laying stages, four that were replaced during early egg-laying and six during brood-rearing were all readily accepted. A total of 82 additional ANBs were provided.

A slight population decline was anticipated in 1994 due to the poor 1993 reproductive success, but the observed 65 percent decline to eight pairs was most discouraging (De Smet 1994). A brochure and information request sent to 4,000 households in southwest Manitoba resulted in only two valid sightings. Some encouragement was afforded by five of the eight pairs selecting ANBs. Two other pairs were relocated into ANBs. This, plus some supplemental feeding during wet, cool weather, resulted in excellent nest success (the eight nesting pairs produced twice as many young as had been produced by 23 pairs in 1993). Over 100 additional ANBs were provided. A total of 20 one-year-old owls from Alberta and Ontario were released. Despite a late release due to export problems, at least six pairs nested and two pairs raised young (including a two female-one male "three-some"). A native prairie/

endangered grassland bird preserve was acquired in extreme southwest Manitoba. Habitat leases were curtailed; this program, now conducted through the Critical Wildlife Habitat Program (CWHP), had resulted in a total of 67 sites (3,455 ha) being temporarily secured for threatened grassland birds. Nineteen CWHP-leased sites supported Burrowing Owls; these 19 sites harbored nearly half of the Burrowing Owls (90 pairs and 17 singles) found during this study.

As Burrowing Owl populations continued to dwindle in 1995 and 1996, monitoring and management were reduced. Surveys included checking previously-used sites, ANBs, and public reports. Four pairs were found in 1995 and only one in 1996 (De Smet 1995, 1996). Extremely low Burrowing Owl densities were also suggested by the scarcity of public reports which arose from newspaper articles, posters, information booths, public presentations and discussions with landowners. Banding of young and adults was also reduced—from 1987-1996, 87 percent of the young were banded and at least 48 percent of the nesting adults were or had been previously banded. Releases in 1995 followed a less labor-intensive technique used in British Columbia where no holding or familiarization pens were employed, but the seven 1-year-old owls all vanished overnight. In 1996, 11 owls from Ontario were released using traditional techniques; five pairs nested including a wild-release pair and threesome, but again only one pair raised young. Given the low reproductive success and poor return rates for released owls, reintroductions were discontinued.

NEST AND TERRITORY REOCCUPANCY

Early studies contended that Burrowing Owls were usually philopatric to nest sites, returning to the same nest year after year. Banding data from this and other recent studies, however, reveal that most burrows are used only once and that what appears to be returning owls are often a totally different pair (Rich 1984, Schmutz 1988, Wellicome and Haug 1995). Of 152 different nest burrows used from 1987-1995, only 26 (17 percent) were reused (including 6 that were reoccupied by unmated adults). Overall, 32 of 179 nests (18 percent) were reused in successive years. Territory reuse was also minimal as only 38 of 101 nesting locales were reused; 39 percent were reoccupied in consecutive years, but less than one-third (32 percent) were reused by nesting pairs.

Percentages that returned to successful nest sites differed from percentages returning to unsuccessful sites. Successful nests were more than three times as likely to be reoccupied the following year (28 of 122; 23 percent) than failed nests (4 of 57; 7 percent). Percentages that returned to the same territory (but not the same nest) were four times greater for successful (28 percent) than for unsuccessful nests (7 percent). Combining nest and territory returns, 51 percent of successful sites were reoccupied compared to only 14 percent of unsuccessful sites.

Preference for ANBs over natural burrows was demonstrated by the frequency with which ANBs were selected even when abundant natural burrows were available. Owls that selected ANBs were often unbanded suggesting no previous exposure to ANBs. Despite six ANBs in 1993 that failed due to weather-related causes and were not reused, the 44 percent reoccupancy rate for ANBs in consecutive years (n=27) greatly exceeded the 13 percent rate observed for natural nests (n=152). Less than 1 percent of natural nests were used for more than 2 consecutive years (one used for 3 years), as compared to 13 percent for ANBs (including one used for 4 and another for 5 years in succession). Although no failed natural nest was reused during this study, four ANBs were reused the following year and another was reoccupied 2 years after it had failed.

RETURN RATES AND MOVEMENTS

Low return rates for banded owls from 1987-1996 point to low adult and juvenile survivorship as the underlying cause of observed declines in Manitoba. Only 3.5 percent of 538 banded young from natural nests returned (11 males, 9 females). The overall return rate for banded adults was 32.7 percent; ranging from an average 40.2 percent for males (n=87) to 24.4 percent for females (n=78). Much lower return rates were recorded for released Burrowing Owls during the present study (0.6 percent for 169 juveniles; 0 percent for 18 adults, 69 one-year-olds and 9 young raised by released pairs).

Although some owls probably returned but were not found and others may have nested at sites outside of the study area, studies conducted in a similar fashion elsewhere have noted higher return rates for young and adults. In Saskatchewan, for example, James *et al.* (in press) reported adult return rates of 37-51 percent. They noted that these return rates, which they incorrectly equated to survival rates, were much lower than survival rates for other similar-sized raptors (Newton 1979), but similar to rates for other declining Burrowing Owl populations. Adult return rates for study areas in Alberta (47-58 percent; Schmutz 1988) and for non-migratory populations in Florida (59-68 percent; Millsap and Bear 1992) and California (81 percent; Thomsen 1971) were even higher, suggesting abnormally low return rates and low year-to-year survival of adult owls from Manitoba. Clayton and Schmutz (1995) noted high juvenile mortality in Alberta; the 67 percent mortality rate recorded during the 3-month post-fledging span was similar to 70 percent mortality rates observed for the entire over-winter period in California (Thomsen 1971) and equivalent to annual mortality rates for most other small raptors (Newton 1979).

Movements of adults and juveniles from 1 year to the next complicates calculations of survival from return rates. Differences in return rates of adult males and females, for example, may be due to greater movements among females from 1 year to the next resulting in fewer females being re-encountered. Indeed, 16 percent of females had a 2 or more year interval between encounters as compared to 9 percent for males. Returning males (n=35) were also much more inclined to return to the same nest (51 percent) or to within 1 km of their previous year's nest (94 percent), compared to 33 percent and 56 percent for 18 returning females. Adults generally moved after nesting unsuccessfully, but at least three females moved 3-28 km after nesting successfully. The average distance moved by males was 3.0 km, but this was reduced to 0.2 km if a 99 km move was excluded. Females moved an average of 10.9 km. Two extraordinary movements are worth highlighting. A juvenile male banded in the southwest in 1988, was found nesting near Brandon (77 km away) in 1990 and returned unmated to this site in 1991; 2 years later it was re-encountered nesting in the southwest (99 km away). An adult female that was banded in 1989 returned unmated to the same site in 1990 but subsequently moved 52 km (overnight); in 1991 this female nested successfully 45 km from the latter site, and in 1992 it nested at another site 8 km away.

In contrast to adults, returning juveniles were invariably found in sites other than where they were raised. The average juvenile movement from natal sites was 32 km (n=18), ranging from 6-77 km for nine males ($\bar{X}$=29.5) and from 1-67 km ($\bar{X}$=33.7) for nine females. Not included was a 1984 juvenile male that was 120 km from its natal site when initially found in 1988 and a juvenile female from Saskatchewan that was found nesting in Manitoba (a 350 km move). No juvenile exhibited natal fidelity, whereas a study in southern Saskatchewan found that two-thirds of 24 young returned to the same pasture (James, in Haug *et al.* 1993). There was no evidence of greater natal fidelity among juvenile males as was reported in Florida (Millsap and Bear 1992) and in Alberta (Schmutz 1988).

POPULATION MODELS

Survival, productivity and dispersal data are important constituent parameters in population dynamics models. These models highlight stages in the life cycle where conservation actions may be most critical. An overly idealistic model by Thomson (1988) showed that population trends in Manitoba could be reversed given return/survival rates of 80 percent for adults and 20 percent for juveniles, productivity of 5 yg/nesting pair, and all owls mating and nesting to 4 years of age. James *et al.* (in press) used a combination of actual and derived numbers to predict extinction of Burrowing Owls near Regina, Saskatchewan, given observed productivity of 3.3 yg/nesting pair, a 37-51 percent return rate for adults and an estimated survival rate of 20 percent for juveniles.

Despite elevated brood sizes observed during the present study, overall productivity appeared barely adequate for population maintenance. Brood sizes from 1987-1996 ($\bar{X}$=5.1; n=122) exceeded those reported in most other studies, including the 2.9 to 4.9 range listed in Haug *et al.* (1993). Clayton and Schmutz (1995) suggested that reduced reproductive success may be contributing to owl declines in Alberta, presenting evidence of a significant decline in brood sizes from 5.7 in 1986 to 3.5 in 1995. Brood sizes also declined during the present study, dropping from an average 5.5 in 1987-1991 (n=88) to 4.1 in

1992-1996 (n=34), however, much of this decline was attributed to differing weather patterns during the latter period. Including failed nests, the average productivity for the present study was 3.4 yg/nesting pair—similar to that observed by James *et al.* (in press) and well within the range of 1.6-4.9 given in Haug *et al.* (1993).

Percentages of Burrowing Owls that nest are reflected by numbers of unmated owls, age of first breeding and maximum breeding age. From 1987-1996, 21 percent of the sites where Burrowing Owls were found were occupied by unmated "singles". Nesting by 1-year-olds appeared normal, especially among females. Nine returning juvenile females all nested during their first year, whereas only 36 percent of juvenile males nested (three other 1-year-old males were unmated and four were not encountered until their second year). Four banded males during the present study were at least 5 years old when last encountered; the oldest Burrowing Owl recorded in the literature was 8.5 years (Haug *et al.* 1993). Although some populations exhibit frequent mate switching (Haug *et al.* 1993), 92 percent of pairs remained together in Florida (Millsap and Bear 1992). During the present study, mate fidelity was exhibited by four banded pairs that retained the same mate from 1 year to next (one for 3 years), whereas three pairs switched mates despite having nested successfully and all returned to the previous year's nest site.

DISCUSSION

Among various limiting factors that have been blamed for Burrowing Owl declines, losses to predators, vehicles and inclement weather seem to have had the largest influence during the present study (De Smet, in prep.). There was less evidence of declines due to insecticides, shooting or to habitat loss and degradation, but these influences can be harder to detect. Although over 700 suitable nesting pastures have been identified in southwest Manitoba (De Smet 1992a), the quality of these pastures has never been examined.

Westworth and Brusnyk (1990) indicated that landowners frequently fail to report owls because they feel they might be asked to restrict agricultural practices or because of a desire to protect the owls from disturbance. Some have gone so far as to blame current declines on monitoring and management activities, insisting that pairs which do not return have left because they were disturbed and that current declines are directly related to management and public awareness activities. These arguments ignore the fact that Burrowing Owls regularly shift nesting sites, that many adults do not survive the rigours of migration and overwintering, that declines are widespread, and that these declines are not a recent phenomenon. Even unmanipulated populations like those monitored by landowners involved in Operation Burrowing Owl (OBO) are demonstrating precipitous declines. Saskatchewan OBO data for 1987-1993, for example, showed: (a) declines in 88 percent of reported sites; (b) 99 percent of the significant trends were downward; (c) disappearing populations throughout the eastern and northern periphery; and (d) numbers in core sites have dropped drastically (Hjertaas in press). Burrowing Owls show little evidence of being affected by human activities and the species is renowned for its tolerance to human activities. Some of the highest densities occur in areas of intensive development; in many areas it is more common to find nesting pairs along busy roadways and in urban parks, lawns and small farmyard pastures than in remote prairie expanses.

The decline of Burrowing Owls is not unique to Manitoba. Despite intense efforts to reverse declines over the past decade, the species is now essentially extirpated in the province. Other populations across the Canadian Prairies are also exhibiting non-reversible declines. Limiting factors show little sign of reversal. An Alberta Land Base Study, for example, indicated that 93 percent of the prime Burrowing Owl habitat in the province is suitable for agricultural expansion and predicted that much of this habitat could disappear in the next 30-50 years (Westworth and Brusnyk 1990). Unless limiting factors change, it appears inevitable that peripheral populations will continue to be extirpated and that core breeding populations throughout the northern Great Plains are in danger of becoming peripheral and eventually extirpated. Although management efforts have resulted in some local improvements, these efforts can be likened to fixing a leaking radiator—as hard as it is to find the holes, it is even more difficult to plug them before all the water drains out.

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LITERATURE CITED

Clayton, K.M.; Schmutz, J.K. 1995. Dispersal, survival and habitat use by Burrowing Owls in Alberta. Prog. Rep. Saskatoon: University of Saskatchewan. 19 p.

Cuthbert, C.W.; Horton, J.I.; McCowan, M.W.; Robinson, B.G.; Short, N.G. 1990. Birder's guide to southwestern Manitoba. Brandon: Brandon Natural History Society. 99 p.

Davis, S.K. 1994. Cowbird parasitism, predation and host selection in fragmented grasslands of southwestern Manitoba. Winnipeg: University of Manitoba. 77 p. M.S.thesis.

De Smet, K.D. 1991. Manitoba's threatened and endangered grassland birds project, 1990 update. Rep. 91-09. Winnipeg: Manitoba Natural Resources. 20 p. & append.

De Smet, K.D. 1992a. Manitoba's threatened and endangered grassland birds: 1991 update and five-year summary. Rep. 92-03. Winnipeg: Manitoba Natural Resources. 77 p.

De Smet, K.D. 1992b. Manitoba's threatened grassland birds: 1992 summary. Unpubl. Rep. to the Burrowing Owl National Recovery Team.

De Smet, K.D. 1993-1996. Conservation efforts for threatened grassland birds in Manitoba. Unpubl. yearly summaries. Winnipeg: Manitoba Natural Resources.

De Smet, K.D.; Conrad, M.P. 1989. Conservation efforts for threatened and endangered grassland birds in Manitoba, 1989. Winnipeg: Manitoba Natural Resources. 23 p. & append.

De Smet, K.D.; McMaster, G.; Mazur, K. 1992. Cooperative surveys and reintroductions of Burrowing Owls between Manitoba and North Dakota, 1991. Unpubl. Rep. Winnipeg: Manitoba Natural Resources. 11 p.

Haug, E.A. 1991. 1988 Manitoba Burrowing Owl conservation program: status report. In: Holroyd, G.L.; Burns, G.; Smith, H.C., eds. Proceedings of the 2d endangered species and prairie conservation workshop. Nat. Hist. Occas. Pap. 15. Provincial Museum of Alberta: 238-240.

Haug, E.A.; Churchward, C. 1989. 1988 Manitoba Burrowing Owl conservation program. Prog. Rep. Winnipeg: Manitoba Natural Resources. 16 p.

Haug, E.A.; Didiuk, A.B. 1993. Use of recorded calls to detect Burrowing Owls. Journal of Field Ornithology. 64(2): 188-194.

Haug, E.A.; Millsap, B.A.; Martell, M.S. 1993. Burrowing Owl. In: Poole, A.; Gill, F., eds. The birds of North America. Washington, DC: Academy of Natural Sciences. 18 p.

Hellman, S.L. 1994. Breeding habitat for the Loggerhead Shrike (*Lanius ludovicianus*) in south-western Manitoba. Natural Resources Institute practicum. Winnipeg: University of Manitoba. 96 p.

Hiltz, B. 1987. Manitoba Burrowing Owl reintroduction program - 1987. Prog. Rep. Winnipeg: Manitoba Natural Resources.

Hjertaas, D. [In press.] Operation Burrowing Owl in Saskatchewan: the first six years. In: Lincer, J.L., ed. Proceedings of the Burrowing Owl symposium; Sacremento, CA. Journal of Raptor Research Special Publication.

Hjertaas, D.; Brechtel, S.; De Smet, K.; Dyer, O.; Haug, E.; Holroyd, G.; James, P.; Schmutz, J. 1995. National recovery plan for the Burrowing Owl. Rep. 13. Ottawa: Recovery of Nationally Endangered Wildlife Committee.

James, P.C.; Ethier, T.J.; Toutloff, M.K. [In press.] Parameters of a declining Burrowing Owl population in Saskatchewan. In: Lincer, J.L., ed. Proceedings of the Burrowing Owl symposium; Sacremento, CA. Journal of Raptor Research Special Publication.

Lawrence, A.G. 1927. Chickadee notes # 310. Winnipeg: Winnipeg Free Press.

Lawrence, A.G. 1937. Chickadee notes # 872. Winnipeg: Winnipeg Free Press.

Millsap, B.; Bear, C. 1992. Mate and territory fidelity and natal dispersal in an urban population of Florida Burrowing Owls. Journal of Raptor Research 27: 62. Abstract.

Newton, I. 1979. Population ecology of raptors. Vermillion, SD: Buteo Press. 399 p.

Olenick, B.E. 1990. Breeding biology of Burrowing Owls using artificial nest burrows in southeastern Idaho. Pocatello: Idaho State University. M.S. thesis.

Ratcliff, B.D. 1987. Manitoba Burrowing Owl surveys, 1982-1984. Manuscript report 87-15. Winnipeg: Manitoba Natural Resources. 22 p.

Rich, T. 1984. Monitoring Burrowing Owl population: implications of burrow re-use. Wildlife Society Bulletin. 12: 178-180.

Schmutz, J.K. 1988. Conservation biology of Burrowing Owls: survival, habitat use and differences between populations. Unpubl. Rep. Saskatoon: University of Saskatchewan. 22 p.

Seton, E.E.T. 1890. The birds of Manitoba. Proc. U.S. Natl. Mus. 13: 457-643.

Seton, E.E.T. 1893. Additions to the list of Manitoba birds. Auk. 10: 49-50.

Seton, E.E.T. 1908. Recent bird records for Manitoba. Auk. 25: 450-454.

Thomsen, L. 1971. Behavior and ecology of Burrowing Owls on the Oakland Municipal Airport. Condor. 73: 177-192.

Thomson, K.A. 1988. Management of Burrowing Owls in Manitoba: population, distribution and plan for recovery. Natural Resources Institute practicum, Winnipeg: University of Manitoba. 66 p.

Wedgwood, J.A. 1978. The status of the Burrowing Owl in Canada. Committee on The Status of Endangered Wildlife in Canada, Ottawa. 84 p.

Wellicome, T.I.; Haug, E.A. 1995. Updated status report on the Burrowing Owl (*Speotyto cunicularia*) in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa. 23 p.

Westworth, D.A.; Brusnyk, L.M. 1990. Provincial management plan for Burrowing Owls in Alberta—draft. Edmonton: Alberta. Fish & Wildlife Division.

Northern Saw-whet Owls (*Aegolius acadicus*) Captured at Cape May Point, NJ, 1980-1994: Comparison of Two Capture Techniques

Katharine E. Duffy and Patrick E. Matheny [1]

Abstract.—During autumn migration 1980-1994, 1,270 Northern Saw-whet Owls (*Aegolius acadicus*) (NSWO) were captured and banded at Cape May Point, NJ. From 1980-1988, captures were effected by passive mist-netting. From 1989-1994, an audiolure (NSWO territorial song broadcast loudly from dusk to dawn in the trapping area) was used to enhance capture rate. 638 NSWOs were captured with an audiolure during five seasons (3.08 owls/100 net-hours), while 632 NSWOs were captured in nine seasons by passive mist-netting (0.51 owls/100 net-hours). Comparisons of age, mass, weather conditions when peak capture rates occurred, seasonal timing of migration and time of night of capture revealed differences and similarities of results between the two capture techniques. For both capture techniques, the proportion of NSWOs captured that were adults varied from year to year. Without an audiolure, 38 percent were adults (range 13-88 percent). With an audiolure, 42 percent were adults (range 10-58 percent). Discriminant analysis of wing chord-mass values to assign sex showed that females were more likely to be captured irrespective of technique. With an audiolure, the mean mass of NSWOs captured increased as did the proportion of females. With either technique, most captures occurred on the nights immediately following the passage of cold fronts, when high pressure dominated the study area. With either technique, most captures occurred when the wind direction was northwest (west through northeast), although the capture rate when wind direction was southwest through east was greater with an audiolure than during passive netting. Diel timing of the majority of captures shifted from pre-dawn without an audiolure to earlier in the night when an audiolure was employed. Seasonal timing of migration was similar with both techniques.

Landforms concentrate owls during migration as they do diurnal raptors. The Cape May peninsula funnels thousands of raptors each fall including numerous Northern Saw-whet Owls (*Aegolius acadicus*) (NSWO). Diurnal raptor migration may be monitored by a variety of effective techniques including conducting counts and attracting hawks with lures for trapping. Techniques for monitoring owl migration are few, yet effective owl monitoring is necessary for conservation. Counting owls has severe limitations (Russell *et al.* 1991). Traditional hawk trapping methods depend on the ability of the raptor to see a lure, often from a great distance. Consequently, most owl capture has been passive, with numerous mist nets placed where owls were likely to be during migration.

The development of a new capture method, the audiolure, revolutionized NSWO monitoring during migration (Erdman and Brinker 1997). When an audiolure, consisting of the territorial song of an NSWO broadcast loudly from dusk to dawn, was used at a trap site, the capture rate increased markedly.

For the past few decades, several stations have monitored owl migration in the Great Lakes area within or near prime NSWO breeding habitat. These stations first captured owls passively, but switched to using an audiolure in the late 1980s. At Cape May, NJ, owls have been captured since 1969 (Clark 1972), at that

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time the only station conducting fall migration monitoring outside NSWO breeding range. Since 1991, several stations in the middle Atlantic states have monitored fall owl migration using audiolures. Cape May is the only owl migration station in the mid-Atlantic area where large numbers of NSWOs have been captured both passively and with the aid of an audiolure. In this paper we compare age, sex, mass, diel timing of migration, weather during peak captures and seasonal timing of migration for NSWOs captured by each method.

STUDY AREA AND METHODS

Owls were captured at six locations (Duffy and Kerlinger 1992) near the tip of the Cape May peninsula in New Jersey, USA (38°56'N, 74°58'W) (fig. 1). From 1980 through 1988, banding efforts began between 28 September and 10 October (median date = 1 October) and ended between 22 November and 5 December (median date = 26 November). From 1989 through 1994, banding efforts began between 7 and 28 October (median date = 23 October) and ended between 15 and 26 November (median date = 19 November).

Capture effort (number of nets and net-hours) and use of each of the six sites varied from year to year during 1980-1988 because of flooding, succession, changes in land ownership and other habitat modifications. From 1989-1994, the results of capture efforts at a site using an audiolure are reported here. During most years from 1989 and 1994, the study site was located in the South Cape May Meadows, although a nearby cultivated field was used in 1989, and a hay field was used in 1991 after the South Cape May Meadows study site was flooded.

The number of nets used each year and the number of nights of operation varied (table 1). The audiolure, a territorial song of a male NSWO recorded on a loop tape and broadcast at a volume sufficient to be heard 0.8 km distant, was located within a square made of four mist nets. Three or four additional mist nets in a line extended from one side of the square and up to eight other mist nets were located within 0.15 km. In 1989 the audiolure was located behind a line of 11 mist nets.

Nets were opened at sunset, closed approximately one hour before sunrise and checked at 1-2 hour intervals; net checks were conducted more frequently on nights when many owls were captured and when temperatures were ≤ 5°C. Nets were not operated during fog or precipitation or when winds were ≥ 30 km-h^{-1}. NSWOs were banded with U.S. Fish and Wildlife Service aluminum leg bands, measured (mass and unflattened wing chord) and aged. Adult (AHY = after hatch year) owls have more than one generation of flight feathers, whereas juveniles (HY = hatch year) have only one generation of flight feathers. The pattern of retained old feathers was recorded for AHY owls.

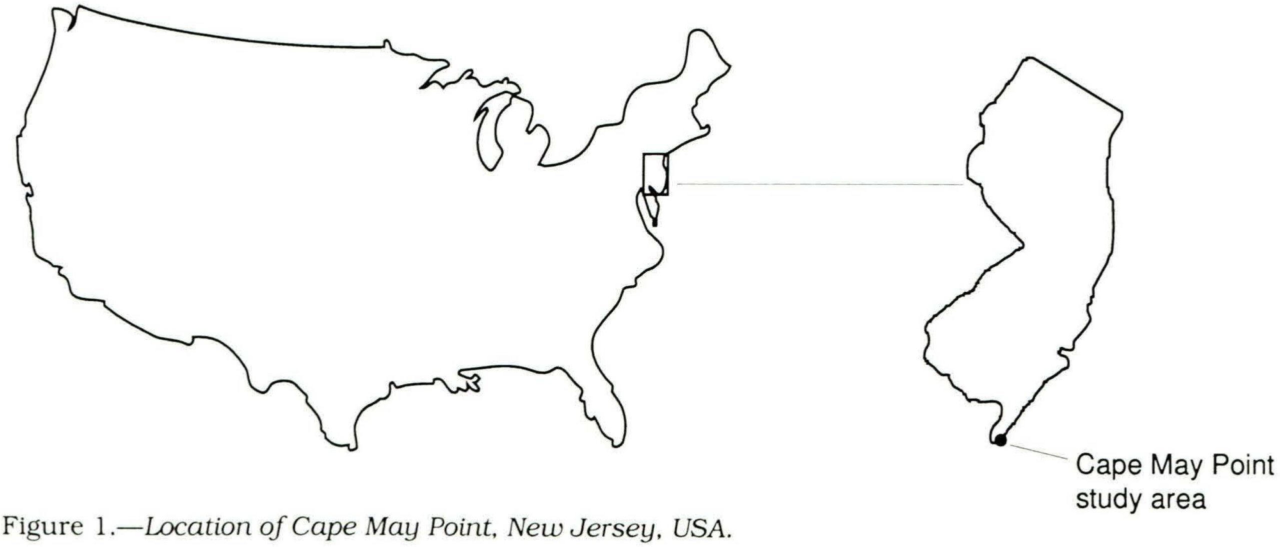

Figure 1.—*Location of Cape May Point, New Jersey, USA.*

Table 1.—*Summary of Northern Saw-whet Owls banded and netting-effort with passive mist-netting, 1980-1988, and with audiolure, 1989-1994, Cape May Point, NJ.*

Year	N	Number of nights	Net-hours	Owls/100 net-hours
Passive				
1980	115	46	11,375	1.01
1981	109	47	15,552	0.7
1982	53	36	9,767	0.54
1983	79	44	12,765	0.62
1984	8	49	26,173	0.03
1985	30	40	23,870	0.13
1986	78	49	17,329	0.45
1987	73	44	17,119	0.43
1988	87	38	12,413	0.7
Total	632	393	146,363	
Mean	**70.2**	**43.7**	**16,263**	**0.51**
SD	32.9	4.4	5,287	0.28
Audiolure				
1989	136	31	5,453	2.49
1990	136	23	3,489	3.9
1991	82	23	2,770	2.96
1992	24	17	1,632	1.47
1993	187	28	3,300	5.67
1994	73	23	3,658	2.0
Total	638	145	20,302	
Mean	**106.3**	**24.2**	**3,387**	**3.08**
SD	52.8	4.4	1,141.7	1.38

ANOVA for owls/100 net-h captured by passive mist-netting and with an audiolure: F=25.28, P<0.01

RESULTS AND DISCUSSION

Use Of Audiolure

Passive mist netting from 1980-1988 resulted in the capture of 632 NSWOs, while use of an audiolure accounted for the capture of 638 NSWOs from 1989-1994 (table 1). From 1980-1988, all migratory owls were considered target species for this study. With the advent of the audiolure, NSWOs became the focus of this monitoring study; starting and ending dates were chosen to take advantage of peak NSWO migration (Duffy and Kerlinger 1992).

When an audiolure was used, less capture effort was required: nights of operation were reduced and fewer mist nets were used (table 1). However, the number of NSWOs captured varied dramatically from year to year. The annual variation does not only reflect netting-effort, but may be due to prevailing fall weather patterns and other factors, e.g., nest success rate for NSWOs in the migratory population.

The audiolure effectively attracts NSWOs—most are captured in nets in closest proximity to the audiolure, which is consistent with the results obtained by Erdman and Brinker (1997). When the audiolure was moved experimentally in 1989, the majority of captures shifted to the nets nearest the new location of the audiolure.

Age

The proportion of adults captured each year fluctuated (table 2). Without an audiolure, 13-88 percent of the NSWOs were adults (mean = 38 percent). With an audiolure, 10-58 percent were adults (mean = 42 percent). An analysis of variance showed that there was no significant difference in the age structure of owls captured with either technique (F = 0.08). Most adults with both capture techniques displayed a molt pattern that indicated they were second-year birds (Evans and Rosenfield 1987, Duffy unpubl. data).

Sexing of NSWOs

The mean mass of NSWOs captured with the audiolure is slightly greater (table 2). From 1980-1988, mean weight of NSWOs captured at Cape May was 89.8 g; from 1989-1994, the mean weight was 92.1 g an increase of 2.3 g. The difference in mass between NSWOs captured passively and those captured with an audiolure was significant (F = 7.32, P < 0.025). NSWOs are sexually dimorphic, so the difference in mass is attributed to the increase in the proportion of females captured (table 3). As in Tengmalm's Owls (*Aegolius funereus*) and other owls, sexual dimorphism in NSWOs is manifested mostly as a difference in mass (Korpimaki 1987, McGillivray 1987). Comparison of our data with the discriminant analysis devised by Brinker *et al.* (1997) for determining sex of NSWOs based on their mass and wing chord showed that the mean mass of females captured by either technique and the mean mass of males captured by either technique were not significantly different (table 3). The increase in the proportion of females captured with an audiolure was significant (table 3).

Our capture data with and without an audiolure suggested that NSWOs may experience a differential migration, with females wintering farther south than males (Brinker *et al.* 1997). Analysis of data on NSWOs captured during migration along the East Coast north and south of Cape May may offer insights on the differential migration hypothesis. Several owl stations have been operated south of Cape May (Brinker *et al.* 1997) for the past few years; a few additional owl monitoring stations were established north of Cape May in 1996. However, when Loos and Kerlinger (1993) sexed by dissection 41 NSWO road-kills found in the Cape May area primarily in winter, they found that only 20 (49 percent) were female. The wintering population may have a 1:1 sex ratio.

Table 2.—*Age and mass of Northern Saw-whet Owls (NSWO) captured at Cape May Point, NJ.*

Year	N	% AHY	Mean Mass (g)
Passive			
1980	115	18	90.4
1981	109	33	89.6
1982	53	59	88.5
1983	79	34	85.8
1984	8	88	92.0
1985	30	13	91.2
1986	78	23	91.1
1987	73	43	90.3
1988	87	35	89.5
Mean	**70.2**	**38**	**89.8**
SD	32.9	22	1.7
Audiolure			
1989	136	53	92.2
1990	136	35	91.4
1991	82	56	91.3
1992	24	58	91.7
1993	187	10	91.7
1994	73	38	94.4
Mean	**106.3**	**42**	**92.1**
SD	52.8	17	1.1

ANOVA (F=0.08) showed that there was no significant difference between NSWO captured with each technique in regard to age; ANOVA (F=7.32, P<0.025) showed that there was a significant difference between NSWO captured with each technique in regard to mass.

Diel Timing of Migration

The diel timing of capture has changed with the use of an audiolure. During passive mist-netting, 26 percent of NSWOs were captured during the first 4-hour period of the night, 33 percent during the second 4-hour period and 40 percent during the last 4-hour period (fig. 2). With an audiolure, the majority of captures occurred during the first two 4-hour periods, 35 percent and 36 percent, respectively, while only 28 percent were caught during the last 4-hour block (fig. 2); X^2 = 19.16, P < 0.0001.

Table 3.—*Sex of Northern Saw-whet Owls captured at Cape May Point, NJ based on discriminant analysis (Brinker* et al. *1977).*

Year	% Male	Mean Male Mass (g)	% Female	Mean Female Mass (g)	N[1]
Passive					
1980	19	79.3	65	95.0	115
1981	18	79.5	66	94.0	109
1982	29	78.5	56	94.9	52
1983	35	77.0	50	92.2	78
1984	0		88	93.7	8
1985	23	80.6	63	96.4	30
1986	18	78.4	65	96.4	77
1987	25	78.9	67	95.6	73
1988	19	78.4	68	93.3	84
Mean	**21**	**78.8**	**65**	**94.6**	
SD	9.1	0.98	9.7	1.35	
Audiolure					
1989	13	79.1	78	95.4	136
1990	13	78.7	77	94.4	129
1991	12	76.3	81	94.1	81
1992	17	77.3	83	94.6	24
1993	13	79.0	76	94.8	187
1994	10	79.9	86	96.6	72
Mean	**13**	**78.4**	**80**	**95.0**	629
SD	2.1	1.21	3.5	0.83	

[1] N included only those individuals for which both wing chord and weight were measured and recorded.
ANOVA showed that the differences in mass of males and females captured with and without an audiolure were not significantly different. ANOVA showed that the increase in the proportion of females captured with an audiolure was significant ($F=11.1$, $P<0.01$), but that the decrease in the proportion of males with an audiolure was not significant.

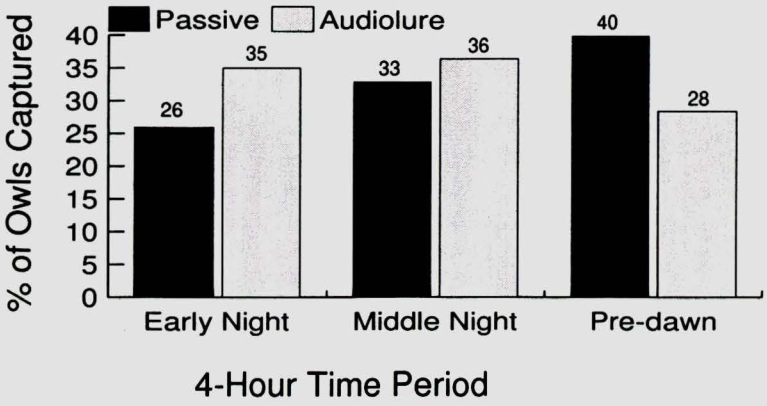

Figure 2.—*Diel timing of Northern Saw-whet Owls captured at Cape May Point, NJ by passive mist-netting and with an audiolure.*

Mist nets only capture NSWOs flying ≤ 2.5 m above the ground. Without an audiolure, the highest capture rate in the last third of the night might be a result of capturing migratory owls actively hunting or seeking a daytime roost. The higher capture rate earlier in the night with an audiolure might be due to the audiolure attracting NSWOs that are migrating (Brinker *et al.* 1997).

Seasonal Timing of Migration.

Migration of NSWOs begins in mid-October and continues throughout November, with peak migration occurring during the first half of November (fig. 3). When NSWOs captured during the peak migration period in 1980-1988 were compared with NSWOs captured using an audiolure during the same time periods in 1989-1994, two differences appeared. With an audiolure, the proportion of NSWOs caught during 26-30 October has decreased. There has also been a significant increase in the NSWOs caught during 5-9 November when an audiolure was employed ($X^2 = 37.0$; $P < 0.0001$).

The reason(s) for the shift in captures noted during 26-30 October and 5-9 November is unknown. The increase in captures in the latter period was so great that it dampened the relative magnitude of captures occurring during other time intervals.

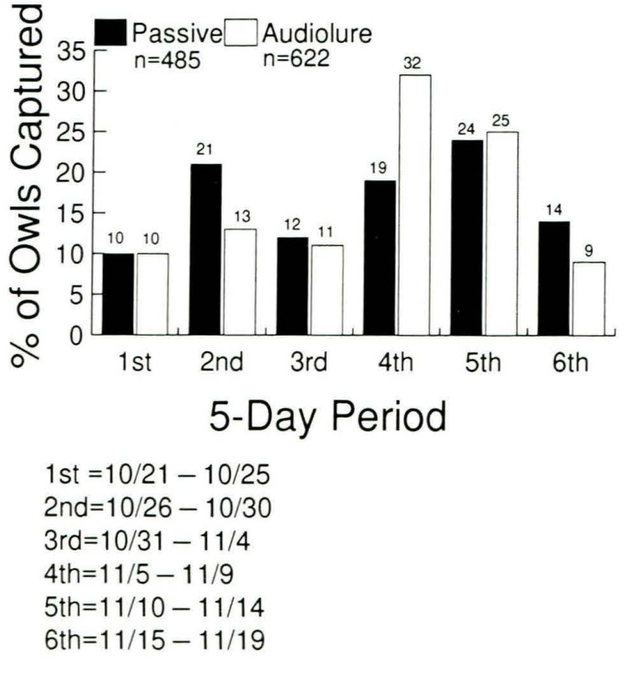

Figure 3.—*Seasonal timing of Northern Saw-whet Owl migration at Cape May Point, New Jersey.*

Weather

Most NSWO captures occurred following the passage of a cold front, when high pressure dominated the study area. Weather conditions propitious for capture were similar to those reported by Evans (1980). With either technique, most captures occurred when the wind direction was northwest (west through northeast). The capture rate when wind direction was less favorable (southwest through east) was greater with an audiolure (20 percent, n = 556) than during passive netting (12 percent, n = 545).

SUMMARY

This study provided a comparison of data on NSWO migration in the mid-Atlantic acquired by passive capture and through the use of an audiolure. Owls captured with each technique did not differ significantly with regard to age, but there was a significant increase in mass and in the proportion of females captured with an audiolure. Time of night of peak capture shifted to earlier in the night with an audiolure. Seasonal timing of capture was similar, although there was a significant increase with an audiolure in the capture rate during 5-9 November. An audiolure augmented captures significantly, warranting its use at all East Coast owl migration stations, especially where a small number of NSWOs pass. Conservation of NSWOs depends upon an improved knowledge of the distribution of these secretive forest owls during all aspects of their life history, so monitoring at additional sites in the Northeast and mid-Atlantic during migration is encouraged.

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LITERATURE CITED

Brinker, D.F.; Duffy, K.E.; Whalen, D.M.; Watts, B.D.; Dodge, K.M. 1997. Autumn migration of Northern Saw-whet Owls (*Aegolius acadicus*) in the middle Atlantic and northeastern United States: what observations from 1995 suggest. In: Duncan, J.R.; Johnson, D.H.; Nicholls, T.N., eds. Biology and conservation of owls of the northern hemisphere: 2d international symposium; 1997 February 5-9; Winnipeg, Manitoba. Gen. Tech. Rep. NC-190. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station: 74-89.

Clark, W.S. 1972. Migration trapping of hawks (and owls) at Cape May, New Jersey—fifth year. Eastern Bird Banding Association News. 35: 121-131.

Duffy, K.; Kerlinger, P. 1992. Autumn owl migration at Cape May Point, New Jersey. Wilson Bulletin. 104(2): 312-320.

Erdman, T.C.; Brinker, D. 1997. Increasing mist net captures of migrant Northern Saw-whet Owls (*Aegolius acadicus*) with an audiolure. In: Duncan, J.R.; Johnson, D.H.; Nicholls, T.N., eds. Biology and conservation of owls of the northern hemisphere: 2d international symposium; 1997 February 5-9; Winnipeg, Manitoba. Gen. Tech. Rep. NC-190. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station: 533-544.

Evans, D.L. 1980. Multivariate analyses of weather and fall migration of Saw-whet Owls at Duluth, Minnesota. Fargo, ND: North Dakota State University. 49 p. M.S. thesis.

Evans, D.L.; Rosenfield, R. 1987. Remigial molt in fall migrant Long-eared and Northern Saw-whet Owls. In: Nero, R.W.; Clark, R.J.; Knapton, R.J.; Hamre, R.H., eds. Biology and conservation of northern forest owls: symposium proceedings;1987 February 3-7; Winnipeg, Manitoba. Gen. Tech. Rep. RM-142. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest Experiment Station: 209-214.

Korpimaki, E. 1987. Sexual size dimorph-ism and life-history traits of Tengmalm's Owl: a review. In: Nero, R.W.; Clark, R.J.; Knapton, R.J.; Hamre, R.H., eds. Biology and conservation of northern forest owls: symposium proceedings; 1987 February 3-7; Winnipeg, Manitoba. Gen. Tech. Rep. RM-142. Fort Collins, CO: U.S. Department of Agricul-ture, Forest Service, Rocky Mountain Forest Experiment Station: 157-161.

Loos, G.; Kerlinger, P. 1993. Road mor-tality of saw-whet and screech-owls on the Cape May peninsula. Journal of Raptor Research. 27(4): 210-213.

McGillivray, W.B. 1987. Reversed size dimorphism in 10 species of northern owls. In: Nero, R.W.; Clark, R.J.; Knapton, R.J.; Hamre, R.H., eds. Biology and conservation of northern forest owls symposium; 1987 February 3-7; Winnipeg, Manitoba. Gen. Tech. Rep. RM-142. Fort Collins, CO: U.S. Department of Agricul-ture, Forest Service, Rocky Mountain Forest Experiment Station: 59-66.

Russell, R.; Dunne, P.; Sutton, C.; Kerlinger, P. 1991. A visual study of migrating owls at Cape May Point, New Jersey. Condor. 93: 55-61.

Habitat Associated with Barred Owl (*Strix varia*) Locations in Southeastern Manitoba: A Review of a Habitat Model

James R. Duncan and Amy E. Kearns[1]

Abstract.—A Habitat Suitability Index (HSI) model was developed for the Barred Owl (*Strix varia*) in southeastern Manitoba. An initial validation of the model was performed within three sizes of circular plots (314, 1,256, and 2,827 ha) centered on 28 Barred Owl locations. The model was able to predict suitable habitat at the 314 ha scale. Forest habitat characteristics within the 314 ha plots were described to suggest improvements to the model's performance. The observed values of the three forest resource inventory variables used in the HSI model; cutting class, crown closure, and tree species composition were generally consistent with the model's predictions. The HSI model emphasized the relative importance of white spruce (*Picea glauca*). This species, while present in the study area, was not detected in the habitat association analysis. A site classification variable not used in the HSI model may have some predictive value. Some of the land units identified as "unproductive areas" may also be important to Barred Owls. Data on the Barred Owl's nesting ecology and actual home ranges are required to further validate the model. Quantifying linkages between Barred Owl habitat and viable population statistics would foster more effective forest management for this species.

Habitat Suitability Index (HSI) models are hypotheses of species-habitat relationships. They are among the most influential management tools in use today (Brooks 1997). Incremental improvements in the modelling process, from development through validation, is recommended and facilitated by publishing interim models that have not been completely validated (Brooks 1997). This paper briefly reviews the development and initial validation of a Barred Owl (*Strix varia*) HSI model for Manitoba and then describes forest habitat associated with 28 Barred Owl locations to suggest improvements to the model.

The Barred Owl (*Strix varia*) is a wide ranging species found in relatively heavy, mature woods, varying from upland forests to lowland swamps in North America (Johnsgard 1988). Godfrey (1986) described its range as: *"Southern wooded Canada (from eastern British Columbia east to Nova Scotia) southward through the United States (east of the Rocky Mountains), and the mountains of Mexico to western Guatemala and Honduras."* The Barred Owl is considered uncommon in Manitoba (Duncan 1996b); it is estimated that there are approximately 1,000-1,500 Barred Owls in the province (Duncan 1994). At least 80 Barred Owl locations have been identified in Manitoba, yet only three Barred Owl breeding occurrences have been documented (Duncan 1994).

Changes in forest landscapes have had a profound effect on endemic wildlife, including the Barred Owl. It has only recently (early 1900's) expanded its range westward into British Columbia, Alaska, Washington, Oregon, Montana, and northern California (Dunbar *et al.* 1991, Grant 1966, Hamer *et al.* 1994, Jones 1987, Munro and Cowan 1947, Oeming and Jones 1955, Shea 1974, Simpson 1915, Taylor and Forsman 1976) from the east via Saskatchewan and Alberta. While the timing and cause of this expansion is questionable, human-induced habitat change (conversion of pure coniferous forest to mixed wood forest as a result of forest harvesting) is cited as the main reason (Allen 1987, Voous 1988).

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Conversely, the Barred Owl is also vulnerable to habitat loss from forest harvesting (Van Ael 1996). Mazur *et al.* (1997) describe it as an old growth dependent species. Barred Owl populations in southern Ontario have likely been severely reduced over the last 150 years as a result of habitat loss and forest fragmentation (Austen *et al.* 1994). Forest fragmentation has also had a negative impact on the Barred Owl in New Jersey (Bosakowsky *et al.* 1987). In order to address these concerns, Barred Owl HSI models have been developed to integrate wildlife habitat values in forest management planning (Allen 1987, Manitoba Forestry Wildlife Management Project [MFWMP] 1994, Olsen *et al.* 1996).

HSI MODEL DEVELOPMENT

The HSI model for the Barred Owl in Manitoba was developed based on a habitat use literature review (Duncan 1994) and focused on its reproductive cover requirements (MFWMP 1994). The assumption was that if the Barred Owl's reproductive cover requirements were met then all of its life requisites would be similarly met. The rationale for developing the model was to put information about Barred Owl habitat use into a form compatible with existing Manitoba forest resource inventory (FRI) data. The Manitoba Barred Owl HSI model is expressed as the interaction between three FRI variables cutting class (V1), canopy closure (V2) and tree species composition (V3) as follows: $HSI = (V1 \times V2 \times (V3^{1/2}))^{.5}$. Cutting class and canopy closure are variables used to describe forest age distribution. Species composition was simplified to reflect the percent conifers within a forest stand.

Forest Resource Inventory Variables

Cutting Class (V1)

According to Natural Resources Manitoba (1996), cutting class is a forest variable based on "*... size, vigor, state of development and maturity of the stand for harvesting purposes; the variable is interpreted from aerial photographs and ground truthing.*" Cutting class is subdivided into five separate categories from one to five (table 1, appendix 1). Cutting class relates to the relative age distribution of each forest stand; it was designed to express the age of a stand with respect to its rotation age. Rotation age is the time at which a stand is ready for harvesting. In Manitoba, rotation age varies from 60 to 140 years. Rotation ages of 140 years are generally reserved for poor and wet sites with slow growth. Using rotation age as a harvesting criteria, overmature stands are defined as any stand 10 years over rotation age. These stands are designated as high priority sites for timber harvesting. The HSI model stated that the Barred Owl was associated with canopy heights > 23m. Consequently, class 3 was estimated to be of very limited value to the Barred Owl only at its upper age/size limit, and then increasingly so for classes 4 and 5 (fig. 1).

Crown Closure (V2)

The second forest variable used in the model is crown closure. It is defined as "*... a variable estimated from aerial photographs. Four classes are recognized and entered for each stand type aggregate. Changes to the estimate*

Table 1.—*Mean area (ha) represented by each cutting class for a series of 28 circular 314 ha plots in southeastern Manitoba containing at least one Barred Owl (*Strix varia*).*

Cutting (age) class	Mean area	95 percent C.I.	S.D.
0 Grass/forb	14.1	6.5	17.5
1 Shrub/seedling (<3m)	35.8	17.6	47.6
2 Pole/sapling (>3m)	44.4	22.6	60.9
3 Intermediate (>10m)	170.5	50.8	137.1
4 Mature	59.5	24.9	66.1
5 Overmature	42.1	27.4	75.2
Unproductive forest	115.8	29.9	80.7

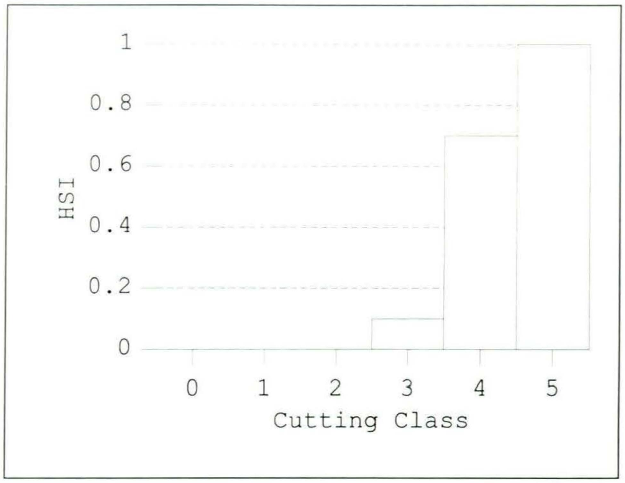

Figure 1.—*Manitoba Barred Owl (*Strix varia*) habitat suit-ability index (HSI) for cutting class (variable 1). Class 0 = grass/forb, 1 = shrub/seed-ling, 2 = pole/sapling, 3 = intermediate, 4 = mature, and 5 = overmature (modified from MFWMP 1994).*

can be only made under exceptional circumstances." Crown closure classes are defined as Class 0: 0-20 percent crown closure; Class 2: 21-50 percent; Class 3: 51-70 percent; and Class 4: >70 percent. The Barred Owl was thought to avoid code 0 and increasingly prefer codes 2 to 4 (fig. 2). [N.B. Code 1 is not defined and does not exist in the FRI database].

Species Composition (V3)

The third forest variable, species composition, is based on "... *the tree count (basal area), for each species in relation to the total tree count (basal area) of the stand expressed as a percentage. It is calculated to the nearest 1/10 percent for a species group determination and then rounded to the nearest 10 percent before being entered into the type aggregate."* A stand type aggregate is comprised of the forest cover type, the subtype, site class, cutting class, and lastly crown closure.

Relative to the first two variables, species composition was considered less important to the Barred Owl (MFWMP 1994). Given that in Manitoba the predominant hardwood is aspen (*Populus* spp.), and that shelter in winter can be provided by all conifers except tamarack (*Larix laricina*), this variable was simplified to reflect the percent softwood (fig. 3). Furthermore, when the conifer component of a mixed wood stand is largely white spruce (*Picea glauca*), it was considered to provide even greater opportunities for nesting (MFWMP 1994). Extensive stands of pure to nearly pure deciduous or coniferous trees were thought to be strongly avoided by the Barred Owl. Conversely, it was considered to prefer mixed wood stands (fig. 3). The model predicts the habitat associated with the Barred Owl at the forest stand level. A more in-depth discussion of the

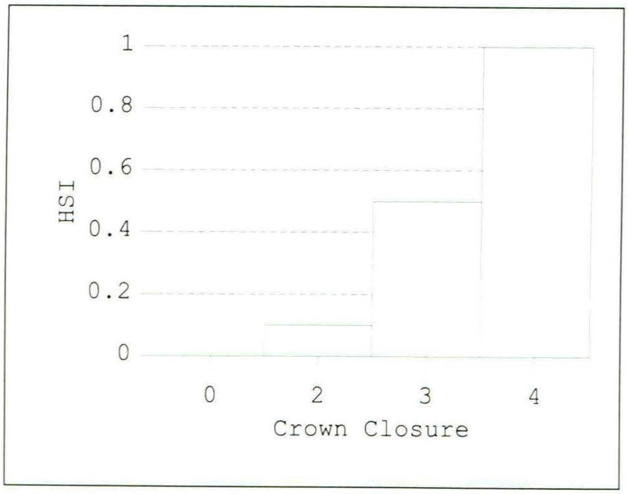

Figure 2.—*Manitoba Barred Owl (*Strix varia*) habitat suitability index (HSI) for crown closure (vari-able 2). Crown Closure 0 = 0-20 percent, 2 = 21-50 percent, 3 = 51-70 percent, and 4 = 71-100 percent (modified from MFWMP 1994).*

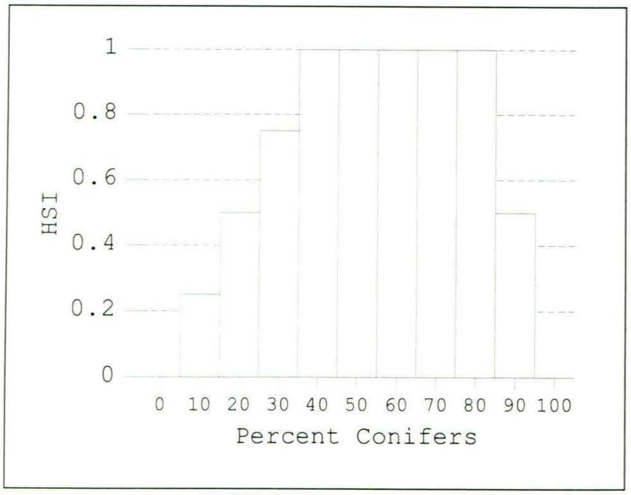

Figure 3.—*Manitoba Barred Owl (*Strix varia*) habitat suit-ability index (HSI) for tree species compos-ition (variable 3). Includes all conifers except tamarack. For all conifers except white spruce, HSI is reduced by 0.5 (modified from MFWMP 1994).*

model can be found in MFWMP (1994) available from the first author.

HSI MODEL INITIAL VALIDATION

Owls were surveyed in southeastern Manitoba using nocturnal surveys in March/April from 1991-1995 (Duncan and Duncan 1997). Individual locations of Barred Owls were determined using triangulation and their location was assigned a latitude and longitude value and digitized into a GIS layer. It was assumed that owls were located within their home range (Duncan 1996a). As a result, a series of concentric circular plots representing the range of reported Barred Owl home range sizes (Duncan 1994) were plotted around each Barred Owl point location. Due to financial and technical constraints, circular plot sizes with radii of 1 km (314 ha), 2 km (1,256 ha) and 3 km (2,827 ha) were chosen.

A series of 94 point locations were randomly generated and digitized into a GIS layer and circular plots of the same size were assigned to these random locations. The model was applied to the FRI to generate HSI values by intersecting the database with the circular plots (Duncan 1996a). HSI values were then calculated for each forest stand polygon within the circular plots. Habitat units (HU) and habitat areas (HA) were calculated for the circular plots at all three spatial scales. Habitat units (HU) were calculated by multiplying the HSI value for each polygon by the polygon's area. A weighted measure of habitat area (HA) was then calculated as the sum of the HU's divided by area and multiplied by 100.

These data were used to make comparisons between Barred Owl and random circular plots. The data failed to approximate a normal distribution (Duncan 1996a), therefore non-parametric tests (Daniel 1978) were used to evaluate the model. Barred Owl plots with 1 km radii had significantly greater median HA values than random plots of the same size ($P = 0.008$, Median Test; $P = 0.034$, Rank Sum Test, Duncan 1996a). Laidig and Dobkin (1995) used a similar technique to evaluate Barred Owl and Great Horned Owl (*Bubo virginianus*) habitat in southern New Jersey.

DESCRIPTION OF ASSOCIATED FOREST HABITAT

In order to more closely examine the model's ability to predict suitable Barred Owl habitat, the description of forest stand variables (cutting class, crown closure, and species composition) in areas associated with Barred Owl locations were tabulated from Manitoba's FRI database. This was limited to the scale (314 ha) at which the model was able to statistically predict habitat suitability (Duncan 1996a). Habitat data were summarized by cutting class, crown closure, species composition and site classification. Site classification was added for this descriptive exercise. The mean, standard deviation and 95 percent confidence intervals were calculated for the variables.

Cutting Class

The Barred Owl typically nests in natural cavities in large deciduous or coniferous trees (Johnsgard 1988). McGarigal and Fraser (1984) indicated that in Virginia it preferred old stands (> 80 years old) rather than young stands (< 80 years old). In the central Appalachians, Devereux and Mosher (1984) determined that eight Barred Owl nest sites were in relatively mature forest stands compared to 76 randomly selected sites. Sutton and Sutton (1985) subjectively noted that in southern New Jersey the Barred Owl was associated with "the oldest growth and uncut stands ... of hardwood forest." In Saskatchewan (Mazur 1997) and Ontario (Van Ael 1996), it preferred mixed-age to mature forests. The consistent relationship between the Barred Owl and older mature forests reflects its need for suitable nesting cavities. These are more likely to be found in large diseased or dying trees. Therefore, substantial areas with older and larger trees (cutting classes 4 and 5) increases the likelihood of the presence of suitable nest structures. However, the most prevalent cutting class associated with the Barred Owl in this study was the intermediate class (table 1). Duncan (1994) suggested that this class was of very limited value in providing nest sites for Barred Owls, except at its upper age/size limit. There are a number of possible explanations why class 3 was so prevalent, and classes 4 and 5 were less abundant.

First, circular plots are likely poor approximations for actual Barred Owl home ranges. Second, large diameter snags with suitable Barred Owl nest sites may be present as residuals within stands designated as cutting class 3. Third, the amount of forest classified as either mature and overmature (table 1) may be sufficient to provide nest sites.

A large proportion of the plots were classified as unforested or unproductive forests (table 1); these areas included treed and untreed muskeg, beaver (*Castor canadensis*) ponds, roads, and other areas not considered in the model.

Crown Closure

The HSI model predicted that the Barred Owl would avoid crown closure code 0, and increasingly prefer codes 2 to 4 (fig. 2). The observed distribution of crown closure classes qualitatively agrees with that prediction; the most prevalent crown class present was the > 71 percent canopy closure class (table 2). However, this is likely related to the corresponding prevalence of immature cutting classes (table 1). The HSI model may possibly be improved by increasing the predicted HSI value of lower crown closure classes for stands that are mature or overmature (cutting class 4 or 5).

Table 2.—*Mean area (ha) represented by each crown class for a series of 28 circular 314 ha plots in southeastern Manitoba containing at least one Barred Owl (*Strix varia*).*

Crown closure class	Mean area	95 percent C.I.	S.D.
0: 0-20 percent	14.1	6.5	17.5
2: 21-50 percent	40.7	16.5	44.4
3: 50-71 percent	84.4	30.1	81.4
4: >71percent	226.7	53.9	145.7
Unproductive forest	115.8	29.9	80.7

Species Composition

There was a wide diversity of general forest cover types present (appendix 2). When tree species composition is simplified to general percentage conifer classes (table 3), the mean area of stands associated with Barred Owl circular plots that are either 'pure' conifer or deciduous is large. The HSI model simplified species composition and predicted that pure or nearly pure stands of deciduous or coniferous trees were relatively unimportant to the Barred Owl, while mixed wood stands were preferred (MFWMP 1994). Because the FRI database rounds percent tree species to the nearest 10 percent, 'pure' conifer stands may actually contain deciduous trees and vice versa. Smaller stands of coniferous or deciduous trees within a mosaic of forest stand types may indeed provide useful habitat. Perhaps the relevance of the tree species composition variable to the predictive ability of the Barred Owl model is minimal.

Table 3.—*Mean area (ha) represented by four general tree species composition classes for a series of 28 circular 314 ha plots in southeastern Manitoba containing at least one Barred Owl (*Strix varia*).*

Species composition[1]	Mean area	95 percent C.I.	S.D.
0 percent conifer	80.4	27.4	73.9
< 51 percent conifer	172.8	45.5	122.8
> 50 percent conifer	35.8	17.2	46.4
100 percent conifer	71.8	36.4	98.2

[1] Conifer = all conifers except tamarack (*Larix laricina*)

Trembling aspen (*Populus tremuloides*) dominated stands had the greatest mean area, followed by black spruce (*Picea mariana*) and tamarack, respectively (table 4). The majority of Barred Owl nests found in North America were in deciduous trees, including aspen (Apfelbaum and Seelbach 1983, Duncan 1994). The relevance of black spruce to the Barred Owl is uncertain; in western Ontario (Van Ael 1996) and central Saskatchewan (Mazur 1997) it strongly avoided lowland black spruce associations. Conversely, anecdotal winter sightings of the Barred Owl in Saskatchewan were almost exclusively in black spruce bogs (W.C. Harris, pers. comm.).

The HSI Model also emphasized the relative importance of white spruce as a source of nest structures (fig. 3), yet this species was not represented (table 4, appendix 2). However, this does not refute the Model's prediction. White spruce is readily detectable from other conifers (except perhaps balsam fir) in aerial photographs, from which FRI data is derived, and is present in the study area, but likely at densities too low (< 10 percent stand volume) to be included in a stand's tree species composition code (G. Peterson, pers. comm.).

While no conclusions about habitat selection can be made from this information, it is interesting to note that the dominant forest cover types (table 4, appendix 2) are often associated with moist sites. Such sites are

Table 4.—*Mean area (ha) represented by dominant tree species composition for a series of 28 circular 314 ha plots in southeastern Manitoba containing at least one Barred Owl (*Strix varia*).*

Dominant tree species composition	Mean area	95 percent C.I.	S.D.
Trembling aspen dominated stands			
100 percent trembling aspen	12.0	6.0	16.2
>50 percent trembling aspen	159.4	46.1	124.5
<50 percent trembling aspen[1]	10.0	4.9	13.1
Black spruce dominated stands			
100 percent black spruce	10.1	4.3	11.5
<50 percent black spruce	62.1	34.0	91.7
Tamarack dominated stands			
100 percent tamarack	8.0	11.1	30.1
>50 percent tamarack	40.5	18.5	50.1
<50 percent tamarack	6.6	5.9	16.0
Other tree species dominated stands			
100 percent jack pine	13.5	16.1	43.4
>50 percent jack pine	8.5	6.4	17.2
>50 percent ash	5.3	6.4	17.2
<50 percent ash	7.7	9.8	26.6
100 percent red pine	5.7	6.3	17.0
<50 percent balsam fir	4.5	6.1	16.5

[1] Other species present in lesser amounts than dominant species.

sometimes associated with a greater diversity of potential Barred Owl prey (Bosakowski *et al.* 1987, Sutton and Sutton 1985). The plots were dominated by a Fresh-wet to Saturated soil regime (table 5). The mean area values for site classification (Barred Owl plots) should be compared to random plots in order to investigate if soil moisture regime is an important variable for the HSI model.

Table 5.—*The mean area (ha) represented by each site classification category for 28 circular 314 ha plots in southeastern Manitoba containing at least one Barred Owl (*Strix varia*).*

Site classification	Mean area	95 percent C.I.	S.D.
Arid-dry	11.1	10.8	29.3
Dry	0.9	2.7	1.0
Fresh-very moist	10.8	9.7	26.2
Fresh-wet	214.8	63.6	171.7
Moist-very moist	2.7	3.4	9.3
Very moist-wet	5.8	3.2	8.7
Saturated	87.4	31.9	86.0
Unclassified	30.6	17.7	47.7
Unproductive forest	115.8	29.9	80.7

CONCLUSIONS

Some cautionary notes regarding interpretations of the observed forest habitat variable distributions are warranted. These values are mean areas for 28 circular plots and do not reflect habitat complexity within and between individual stands of trees. Barred Owl home ranges are irregularly shaped (Mazur 1997); the circular plots associated with Barred Owls likely encompass only a portion of their home range. In addition, 28 Barred Owl locations is not a large enough sample to make statistically powerful conclusions. Nonetheless, the salient and essential elements of Barred Owl habitat may be captured by the current HSI model. Additional research is recommended to further validate and refine the model.

Site classification (soil moisture regime), which is described in part by tree species composition, may be an important variable to incorporate into the model. Currently, the model is unable to evaluate unclassified areas; it ranks these areas as having no value to Barred Owls. The presence of unproductive forests and unclassified areas may in fact enhance breeding success. The model should ideally be revised according to how both biotic and abiotic factors influence breeding success of the Barred Owl in Manitoba.

The interaction between forest cover types within a Barred Owl's home range may influence the habitat's ability to provide critical breeding, foraging and roosting habitat for the Barred Owl. Distance to water, proximity to human habitation and forest fragmentation may influence Barred Owl breeding success and survival.

Change in habitat availability and quality over time and across a given landscape can greatly influence nesting success of the Barred Owl given its high nest site fidelity and territorial nature. Forest cover heterogeneity and contiguity over time should be incorporated into the model to help maintain viable populations of the Barred Owl. Quantifying linkages between Barred Owl habitat and viable population statistics would foster more effective forest management for this species.

ACKNOWLEDGMENTS

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LITERATURE CITED

Apfelbaum, S.I.; Seelbach, P. 1983. Nest tree, habitat selection and productivity of seven North American raptor species based on the Cornell University nest record program. Raptor Research. 17: 97-113.

Allen, A.W. 1987. Habitat suitability index models: Barred Owl. Biol. Rep. 82 (10.143). Fort Collins, CO: U.S. Forest Service, National Ecology Center.

Austen, M.J.W.; Cadman, M.D.; James, R.D. 1994. Ontario birds at risk: status and conservation needs. Federation of Ontario Naturalists & Long Point Bird Observatory. Don Mills, ON: General Printers.

Bosakowski, T.; Speiser, R.; Benzinger, J. 1987. Distribution, density, and habitat relationships of the Barred Owl in northern New Jersey. In: Nero, R.W.; Clark, R.J.; Knapton, R.J.; Hamre, R.H., eds. 1987. Biology and conservation of northern forest owls: symposium proceedings; February 3-7; Winnipeg, Manitoba. Gen. Tech. Rep. RM-142. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 135-143.

Brooks, R.P. 1997. Improving habitat suitability index models. Wildlife Society Bulletin. 25: 163-167.

Daniel, W.W. 1978. Applied non-parametric statistics. 2d ed. Boston, MA.: PWS-Kent Publishing Company.

Devereux, J.G.; Mosher, J.A. 1984. Breeding ecology of Barred Owls in the central Appalachians. Raptor Research. 18: 49-58.

Dunbar, D.L.; Booth, B.P.; Forsman, E.D.; Hetherington, A.E.; Wilson, D.J. 1991. Status of the Spotted Owl, *Strix occidentalis*, and Barred Owl, *Strix varia*, in southwestern British Columbia. Canadian Field-Naturalist. 105: 464-468.

Duncan, J.R. 1994. Barred Owl habitat use literature review. Winnipeg, MB: Manitoba Forestry/Wildlife Management Project.

Duncan, J.R. 1996a. An initial validation of a Barred Owl (*Strix varia*) habitat suitability index model for Manitoba. Winnipeg, MB: Manitoba Forestry/Wildlife Management Project.

Duncan, J.R. 1996b. Conservation status ranks of the birds of Manitoba. Manitoba Conserv. Data Centre MS Rep. 96-05. Winnipeg, MB.

Duncan, J.R.; Duncan, P.A. 1997. Increase in distribution records of owl species in Manitoba based on a volunteer nocturnal survey using Boreal Owl (*Aegolius funereus*) and Great Gray Owl (*Strix nebulosa*) playback. In: Duncan, J.R.; Johnson, D.H.; Nicholls, T.H., eds. Biology and Conservation of owls of the northern hemisphere: 2d international symposium; 1997 February 5-9; Winnipeg, MB. Gen. Tech. Rep. NC-190. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station: 519-524.

Godfrey, W.E. 1986. The birds of Canada, rev. ed. Ottawa, ON: National Museum of Natural Science.

Grant, J. 1966. The Barred Owl in British Columbia. Murrelet. 47: 39-45.

Hamer, T.E.; Forsman, E.D.; Fuchs, A.D.; Walters, M.L. 1994. Hybridization between Barred and Spotted Owls. Auk. 111: 487-492.

Johnsgard, P.A. 1988. North American owls: Biology and natural history. Washington, DC: Smithsonian Institution Press.

Jones, E.T. 1987. Early observations of Barred Owls in Alberta. Blue Jay. 45: 31-32.

Laidig, K.J.; Dobkin, D.S. 1995. Spatial overlap and habitat associations of Barred Owls and Great Horned Owls in southern New Jersey. Journal of Raptor Research. 29: 1515-1517.

Manitoba Forestry/Wildlife Management Project. 1994. Habitat suitability index for the Barred Owl in Manitoba. Winnipeg, MB.

Mazur, K.M. 1997. Spatial habitat selection by Barred Owls in the boreal forest of Saskatchewan, Canada. Regina, SK: University of Regina. M.S. thesis.

McGarigal, K.; Fraser, J.D. 1984. The effect of forest stand age on owl distribution in southwestern Virginia. Journal of Wildlife Management. 48: 1393-1398.

Munro, J.A.; Cowan, I.McT. 1947. A review of the bird fauna of British Columbia. B.C. Prov. Mus. Spec. Publ. 2. Victoria, BC.

Natural Resources Manitoba. 1996. Forest Inventory Field Instruction Manual. Winnipeg, MB: Forest Resources Management.

Oeming, A.F.; Jones, E.T. 1955. The Barred Owl in Alberta. Canadian Field-Naturalist. 69: 66-67.

Olsen, B.; Takats, L.; Beck, B.; Beck, J. 1996. Barred Owls (*Strix varia*) breeding habitat: draft habitat suitability index (HSI) model. In: Beck, B.; Beck, J.; Bessie, W.; Bonar, R.; Todd, M., eds. Habitat suitability index models for 35 wildlife species in the Foothills Model Forest. Draft report. Hinton, AB: Foothills Model Forest: 11-20.

Shea, D.S. 1974. Barred Owl records in western Montana. Condor. 76: 222.

Simpson, R.B. 1915. The Barred Owl. Oologist. 32: 9-10.

Sutton, C.C.; Sutton, P.T. 1985. The status and distribution of Barred Owl and Red-shouldered Hawk in southern New Jersey. Cassinia. 61: 20-29.

Taylor, A.L., Jr.; Forsman, E.D. 1976. Recent range extensions of the Barred Owl in western North America, including the first records for Oregon. Condor. 78: 560-561.

Van Ael, S.M. 1996. Modelling Barred Owl habitat in Northwestern Ontario. Thunder Bay, ON: Lakehead University. M.S. thesis.

Voous, K.H. 1988. Owls of the northern hemisphere. Cambridge, MA: MIT Press.

Appendix 1.—*Manitoba Forest Resource Inventory Cutting Class Variable (Natural Resources Manitoba 1996).*

Cutting class is subdivided into five separate categories from one to five based on size, vigor, state of development and maturity of the stand for harvesting purposes; the variable is interpreted from aerial photographs and ground truthing.

Class 0: Grass/forb: Forest land not restocked following fire, cutting, windfall or other major disturbances (hence potentially productive land). Some reproduction or scattered residual trees (with net merchantable volume less than 20 m^3 per hectare) may be present.

Class 1: Shrub/seedling: Stands which have been restocked either naturally or artificially. There may be scattered residual trees present as in class 0. To be in class 1 the average height of the stand must be less than 3 m.

Class 2: Pole/sapling: Advanced young growth of post size, with some merchantable volume. The average height of the stand must be over 3 m in order to be in this cutting class.

Class 3: Intermediate: Immature stands with merchantable volume growing at or near their maximum rate, which definitely should not be cut. The average height of the stand should be over 10 m and the average diameter should be over 9 cm at d.b.h. (1.3 m above ground).

Class 4: Mature: Mature stands which may be cut as they have reached rotation age. Rotation age is the time at which a stand is ready for harvesting. In Manitoba, rotation age varies from 60 to 140 years. Rotation ages of 140 years are generally reserved for poor and wet sites with slow growth.

Class 5: Overmature: Overmature stands are at least 10 years older than rotation age and should be given a high cutting priority.

Appendix 2.—*Mean area (ha) represented by tree species composition for a series of 28 circular 314 ha plots in southeastern Manitoba containing at least one Barred Owl* (Strix varia).

Tree species[1]	**Mean area**	**95 percent C.I.**	**S.D.**	**Count**[2]
Unproductive forest	115.8	29.9	80.7	28
Tamarack 70; black spruce 30	24.3	12.7	34.4	17
Trembling aspen 70; black spruce 30	21.8	14.6	39.5	11
Black spruce 70; tamarack 30	20.6	16.4	44.2	11
Trembling aspen 80; balsam poplar 20	16.3	4.3	23.0	12
Jack pine 100	13.1	8.1	42.7	6
Trembling aspen 100	12.0	3.1	16.2	17
Black spruce 100	10.1	2.2	11.5	21
TA[3] 70; white birch 20; balsam poplar 10	9.9	5.2	27.3	6
Tamarack 100	8.0	5.7	30.1	6
Black spruce 80; tamarack 20	7.6	3.4	17.8	5
BS[3] 60; eastern cedar 30; tamarack 10	6.0	2.9	15.4	6
TA 60; BP[3] 20; WB[3] 10; balsam fir 10	6.0	3.4	18.3	4
Tamarack 60; black spruce 40	5.8	2.7	14.5	5
Black spruce 90; tamarack larch 10	5.8	2.7	14.4	5
Red pine 100	5.7	3.2	17.0	7
TA 60; white birch 20; balsam fir 20	5.5	2.9	15.2	4
Black spruce 70; trembling aspen 30	5.1	1.8	9.5	10
Tamarack larch 80; black spruce 20	4.9	1.2	6.4	13
Trembling aspen 70; balsam fir 30	4.6	2.1	10.9	8
Trembling aspen 90; balsam poplar 10	3.7	1.9	10.2	7
Trembling aspen 90; jack pine 10	3.1	1.3	6.9	10
Jack pine 80; trembling aspen 20	3.0	1.5	7.9	8
Trembling aspen 80; black spruce 20	2.3	0.9	4.8	9
TA 70; balsam poplar 20; white birch 10	2.2	1.5	7.7	5
TA 70; black spruce 20; balsam fir 10	1.5	0.8	4.0	6
TA 60; balsam poplar 30; balsam fir 10	1.5	0.6	3.1	6
Black spruce 80; trembling aspen 20	1.4	0.6	3.2	8

[1] Main cover species with percentages.

[2] Number of Barred Owl plots with tree species composition group.

[3] TA = Trembling Aspen; BS = Black Spruce; BP = Balsam Poplar; WB = White Birch.

You Are What You Eat: Stable Isotope Ecology of Owl Diets in Alberta, Canada

Jason M. Duxbury and Geoffrey L. Holroyd[1]

Abstract.—Stable isotope ratio analysis (SIRA) was used to analyze the trophic level of the diets of three owl species: Barred Owl (*Strix varia*), Northern Hawk Owl (*Surnia ulula*) and Great Horned Owl (*Bubo virginianus*). Barred Owl and Northern Hawk Owl had diets from a similar trophic level. Both the Barred Owl and Northern Hawk Owl had diets from trophic levels that differed significantly from that of the Great Horned Owl. Great Horned Owl had the most diverse isotope ratios indicating the greatest intraspecific variation in diets of the three species of owls. Results of SIRA can help with the determination of owl diets when used in conjunction with traditional methods of studying diet, but they can also stand alone as indicators of unique diet habits or discerning the trophic level of the diets of museum specimens.

The analysis of the ratio of stable isotopes of selected elements was developed by geologists and geochemists over 60 years ago. Their applications of stable isotope ratio analysis (SIRA) included, but were not limited to, isotope hydrology, tracing geomorphologic pathways and palaeoclimatology (Ehleringer and Rundel 1989). Geochemists were the first to realize that stable isotope ratios changed in biological systems and began to determine how and why the ratios changed (Craig 1953, Park and Epstein 1960, Wickman 1952). Based on the founding work of the geochemists, the fields of archaeology, anthropology, palaeoecology, and contemporary ecology all began to take advantage of the usefulness of stable SIRA for dietary analyses of prehistoric or contemporary systems (Bombin and Muelenbachs 1985, Chrisholm *et al.* 1982, DeNiro 1987, Fry 1988, Minagawa and Wada 1984, Miyake and Wada 1967 [in Ehleringer and Rundel 1989], Schoeninger and DeNiro 1984). The use of SIRA in avian ecology is one of the most recent developments with applications in physiology, trophic level determinations, food web tracing and prey selection studies (Alisauskas and Hobson 1993, Hobson 1993, Hobson and Clark 1992, Hobson and Montevecci 1991, Hobson and Sealy 1991, Mizutani *et al.* 1990, Mizutani *et al.* 1986, Mizutani and Wada 1988, Thompson and Furness 1995).

Two important properties of stable isotopes in animal tissue permit the interpretation of the trophic level of a species' diet. First, stable isotope ratios found in tissue represent an average of all isotopes found in the ingested food which are subsequently used in building the tissues of the organism. Secondly, relatively heavier stable isotopes bioaccumulate with each upward step in a food web system due to catabolic processes that favor the elimination of the relatively lighter isotopes which are excreted (Ehleringer and Rundel 1989, Mizutani and Wada 1988, Peterson and Fry 1987). These two characteristics make SIRA a valuable tool in the dietary analysis of owl species.

The classic techniques to determine the diets of raptors are pellet analysis (Errington 1932) and crop/stomach content analysis (Duncan 1966, Errington 1933, Sherrod 1978), prey remains analysis (Craighead and Craighead 1956, Hunt 1993, Meng 1959), and direct observation

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(Bielefeldt *et al.* 1992, Hunt 1993, Quinn 1991). The species of prey can be identified from the analysis of the contents of owl pellets (Errington 1932, Marti 1974). However, prey with more easily digestible components may be under represented in the analysis. Also, the number of prey items is hard to determine since large prey items may be found in more than one pellet and small prey items may be combined into a single pellet (Mermann *et al.* 1992). Owls may also cache prey, consuming the rest in a subsequent feeding and forming multiple pellets from single prey items (Thomsen 1971).

Stomach or crop content analysis is an excellent way to determine exactly what a raptor has eaten. If the prey is still undigested, it can be accurately identified. However, this technique requires the use of emetics or the death of the predator and provides only single samples of a potentially very variable diet.

Body parts, feathers or fur left at kill sites can provide evidence of prey captures. A list of prey species, their relative abundance and relative contribution to biomass of diet can be determined from prey remains (Bosokowski *et al.* 1992). When avian prey are delivered to the nests of raptors, feathers are plucked and remain in and near the nest allowing the identification of avian prey. When mammals are consumed there is little remaining. The carcasses of both birds and mammals are removed and rarely are found by researchers. The presence of feathers and not fur biases the results in favor of relatively more avian prey than what is actually consumed (Bielefeldt *et al.* 1992, Hunt 1993, Quinn 1991).

Direct observation, if done consistently, allows for a more complete tally of prey taken although specific identification can be difficult for small prey (Bielefeldt *et al.* 1992, Hunt 1993). This technique is also time consuming and compiling a large sample size can be expensive.

Combining the above techniques removes some of the biases, but may not always be temporally, physically, or financially possible. Stable isotope ecology can be applied to enhance these techniques and help interpret their associated biases. SIRA represents the average of the isotopes ingested, and with increasing trophic level there is bioaccumulation of the relatively heavier isotopes. Studies of marine birds demonstrated that the ratio of $^{15}N/^{14}N$ increases by 2 to 4‰ (parts per mil) with each trophic level (Hobson 1993). These ratios are passed on to the consumers in each ecosystem (Fry *et al.* 1978.). SIRA by itself can provide some insights on the diets of birds. However, SIRA used in conjunction with more traditional diet study methods provides a more complete picture of diet.

In a previous experiment using a known food chain at a captive Peregrine Falcon (*Falco peregrinus*) breeding facility, we demonstrated that both $\delta^{15}N$ and $\delta^{13}C$ increased in a stepwise pattern (unpubl. data, fig. 1). Since the samples of wild owls came from different ecosystems, carbon ratios are less important since base levels are determined by the ecosystems that the owls inhabited (DeNiro 1987, DeNiro and Epstein 1978). Therefore, only the bioaccumulation properties of ^{15}N are used in this paper.

To demonstrate how SIRA can be used in owl diet studies, $^{15}N/^{14}N$ ratios in feathers from Northern Hawk Owls (*Surnia ulula*), Barred Owls (*Strix varia*) and Great Horned Owls (*Bubo virginianus*) from the boreal ecoregion of Alberta were analyzed. The difference and variance in trophic levels of prey of owls within and between species, combined with pellet/prey analysis, can provide an interpretation of what possible prey items were being consumed.

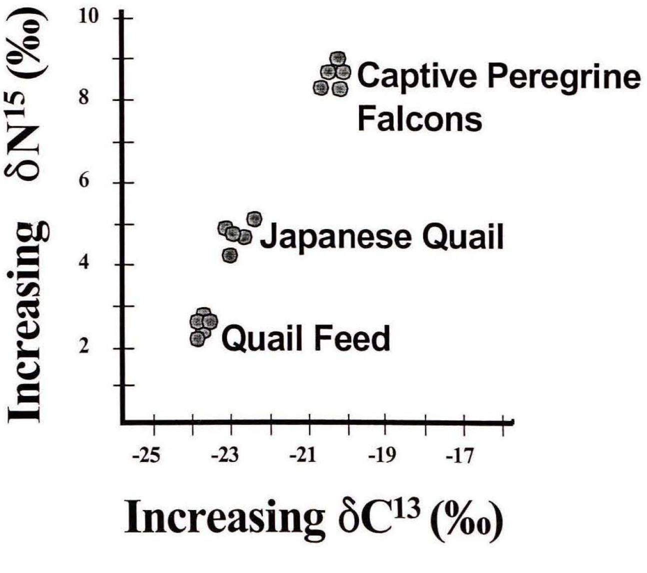

Figure 1.—$\delta^{15}N$ and $\delta^{13}C$ *values of a known food chain of captive Peregrine Falcons and their food source.*

METHODS

Flight feathers were retrieved from road-killed owls, at nest sites, and museum specimens and body feathers were collected from nestlings at the time of banding. Feathers were washed with soap and distilled water to remove debris and external contaminants. To ensure complete combustion of the sample tissue, each feather was then cut into very fine fragments with stainless steel scissors and ground even finer with a mortar and pestle. Incomplete combustion leads to unreliable values resulting from altered ratios (Owens 1987). Fine feather particles were washed with diethyl ether to remove contaminants and lipid tissue. A mass spectrometer needs a minimum amount of sample gas, so the amount of the sample was dependent upon the predicted amount of nitrogen and carbon in the sample tissue: approximately 15 percent nitrogen and 50 percent carbon (Kemp and Rogers 1972, Reed and Woods 1964). About 0.230-0.280 mg per sample were then combusted in an elemental analyzer that was interfaced with a mass spectrometer in a continuous flow mode. A standard of atropine powder was sampled and the analytical error of the mass spectrometer was measured to be ± 0.174‰. All tissues are expressed in δ(delta) notation according to the following formula:

$$\delta^{15}N = \frac{\text{Rsample - Rstandard}}{\overset{(‰)}{\text{Rstandard}}} \times 1000$$

Rstandard is the ratio of the isotopes in the standard (natural air for nitrogen) and **R**sample is the ratio of the isotopes in the sample tissue. The relative amount of naturally occurring heavy isotopes is less than 1 percent, therefore, final numbers are always multiplied by 1,000 and presented in the per mil (‰) notation (parts per thousand).

RESULTS

Stable isotope ratio analysis was performed on 56 Great Horned Owl feathers, 15 Northern Hawk Owl feathers, and 21 Barred Owl feathers (table 1). In increasing relative amount of heavy nitrogen, the Barred Owl had the lowest mean ($\delta^{15}N = 6.845 \pm 1.086$), the Northern Hawk Owl had a mean of ($\delta^{15}N = 7.137 \pm 1.103$) while the Great Horned Owl had the greatest mean ($\delta^{15}N = 8.698 \pm 1.913$). The ranges of $\delta^{15}N$ values for each species in increasing order was found to be 3.8 for Northern Hawk Owls, 4.3 for Barred Owls, and 8.9 for Great Horned Owls. The difference between the isotope ratios in the samples from the Great Horned Owl were statistically higher that for the other two species (Barred Owl: t-test, $p < 0.0001$; Mann-Whitney U, $p < 0.0001$; Northern Hawk Owl: t-test, $p < 0.0002$; Mann-Whitney U, $p < 0.002$). However, the difference between Barred Owl and Northern Hawk Owl ratios was not statistically significant (t-test, $p = 0.4378$; Mann-Whitney U, $p = 0.5962$).

DISCUSSION

Birds feeding at high trophic levels will have a relatively higher ratio of stable isotopes because of the bioaccumulation of heavy isotopes (DeNiro 1987, Fry 1988, Minagawa and Wada 1984, Owens 1987, Wada *et al.* 1987). The mean $\delta^{15}N$ values indicate that the Barred Owls and Northern Hawk Owls sampled in this study were feeding on prey found at relatively lower trophic levels than were the Great Horned Owls that were sampled. However, since most owls concentrate their diets on herbivorous mammals (Earhart and Johnson

Table 1.—*Descriptive statistics for $\delta^{15}N$ values of owl feather samples. All numbers are per mil (‰).*

	Barred Owl	Northern Hawk Owl	Great Horned Owl
Mean (n)	6.845 (21)	7.137 (15)	8.698 (56)
Standard deviation	1.086	1.103	1.913
Maximum	9.100	9.240	13.650
Minimum	4.810	5.470	4.760
Range	4.290	3.770	8.890

1970, Marti 1974, Roth and Powers 1979, Taylor 1984), the isotope values indicate that some of the Great Horned Owls took more prey that were from higher trophic levels (such as birds and insects) than did the owls with feathers with low isotope ratios (fig. 2).

The differences in the variation of isotope ratios within each species indicates the variability of the diet of individual owls. The isotope ratio in each sample represents the average of the trophic levels of a single owl's prey while it grew the feather. The mean and variation in SIRA values of the Barred Owl and Northern Hawk Owl are very similar indicating that their diets are from similar trophic levels and that each owl species is likewise taking prey from a low trophic level. These owls are probably consuming primarily herbivorous rodents supplemented by insectivorous mammals and birds and presumably there is little variation between the diets of all of the individual owls. The higher the SIRA values for a given owl, the more that owl is probably capturing animals located at a relatively higher trophic level.

The range of SIRA values for the Great Horned Owl is almost twice that of both the Barred Owl and the Northern Hawk Owl, supporting literature that the diet of the Great Horned Owl has much more variability than the other two owl species (Aigner *et al.* 1994, Brodie and Maser 1967, Knight and Erickson 1977, Marti 1974, Orians and Kuhlman 1956, Weir and Hanson 1989). The upper range of Great Horned Owl values suggests that these owls are taking second or possibly third trophic level feeders (fig. 2).

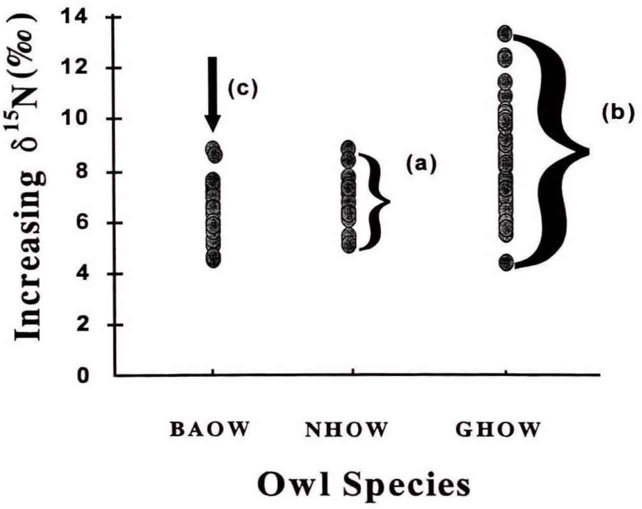

Figure 2.—*$\delta^{15}N$ values of three owl species: Barred Owl (BAOW), Northern Hawk Owl (NHOW) and Great Horned Owl (GHOW). Northern Hawk Owls have a less variable diet (a) than Great Horned Owls (b). Knowing the diet of one Barred Owl can lead to predictions of the prey selection of another Barred Owl with an unknown diet (c).*

The two uppermost samples of Barred Owl demonstrate how SIRA can be used in dietary studies (fig. 2). One owl's diet was studied, while the other had an unknown diet as the feather was removed from a museum specimen. Using traditional diet study methods of pellet and prey remains analysis, the owl with the highest value is known to have consumed a high proportion of birds and frogs (L. Takats, Graduate Student, Department of Renewable Resources, University of Alberta, pers. comm.). Such a diet would produce relatively high SIRA values because of the insectivore habits of the prey. Also, aquatic systems have relatively higher $\delta^{15}N$ values because they contain more trophic levels than terrestrial systems (Goering *et al.* 1990). With this pattern, one may predict that the museum specimen with the unknown diet, had also been consuming insectivores at a frequency comparable to the live owl. Using SIRA in conjunction with traditional methods helps indicate that the birds and frogs may play a vital role in this particular owl's diet. If similar prey items were found in prey remains or pellets near a nest, but the SIRA value of the nesting owls were low, then it could be assumed that these prey items were rarely caught. Caution must be used to make such conclusions without the use of traditional methods along with SIRA, but SIRA can be an indicator of diets that may require closer examination. If an individual owl were still alive, the isotope results may suggest that the researcher return to the study site, reuse traditional methods, but now knowing what possible prey items to look for, potentially making the diet study more complete.

CONCLUSION

The known bioaccumulation properties of ^{15}N can be used to study the diets of any organism. For owls, SIRA can play a very useful role particularly when used with more traditional diet study methods to produce a more comprehensive view of the owls diet. The averaging of isotope ratios helps to reduce some of the biases associated with more traditional diet study techniques. SIRA can be used alone in studies where pellet and/or prey analysis or long-term nest observations are not possible because of temporal, physical, or monetary limitations. It may also be used on specimens to generalize or estimate their diet.

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LITERATURE CITED

Aigner, P.A.; Morrison, M.L.; Hall, L.S.; Block, W.M. 1994. Great Horned Owl food habits at Mono Lake, California. Southwest Natural-ist. 39: 286-288.

Alisauskas, R.T.; Hobson, K.A. 1993. Determination of Lesser Snow Goose diets and winter distribution using stable isotope analysis. Journal of Wildlife Management. 57: 49-54.

Bielefeldt, J.; Rosenfield, R.N.; Papp, J.H. 1992. Unfounded assumptions about diet of the Cooper's Hawk. Condor. 94: 427-436.

Bombin, M.; Muehlenbachs, K. 1985. 13c/12c ratios of Pleistocene mummified remains from Beringia. Quarternary Research. 23: 123-129.

Bosokowski, T.; Smith, D.G.; Speiser, R. 1992. Niche overlap of two sympatric-nesting hawks Accipiter spp. in the New Jersey - New York highlands. Ecography. 15: 358-372.

Brodie, E.D., Jr.; Maser, C. 1967. Analysis of Great Horned Owl pellets from Deschutes County, Oregon. Murrelet. 48: 11-12.

Chrisholm, B.S.; Nelson, D.E.; Schwarcz, H.P. 1982. Stable carbon isotope ratios as a measure of marine versus terrestrial protein in ancient diets. Science. 216: 1131-1132.

Craig, H. 1953. The geochemistry of stable carbon isotopes. Geochimica Cosmochimica Acta. 3: 53-92.

Craighead, J.J.; Craighead, F.C., Jr. 1956. Hawks, owls and wildlife. Harrisburg, PA: Stackpole Co.

DeNiro, M.J. 1987. Stable isotopy and archaeology. American Scientist. 75: 182-191.

DeNiro, M.J.; Epstein, S. 1978. Influence of diet on the distribution of carbon isotopes in animals. Geochimica Cosmochimica Acta. 42: 495-506.

Duncan, S. 1966. An analysis of the stomach contents of some Cooper's Hawks (*Accipiter cooperii*). Auk. 83: 308.

Earhart, C.M.; Johnson, N.K. 1970. Size dimorphism and food habits of North American owls. Condor. 72: 251-264.

Ehleringer, J.R.; Rundel, P.W. 1989. Stable isotopes: history, units, and instrumentation. In: Rundel, P.W.; Ehleringer, J.R.; Nagy, K.A., eds. Stable isotopes in ecological research. Ecological Studies Vol. 68. New York, NY: Springer-Verlag New York Inc.: 1-15.

Errington, P.L. 1932. Technique of raptor food habits study. Condor. 34: 75-86.

Errington, P.L. 1933. Food habits of southern Wisconsin raptors. Part II. Hawks. Condor. 35: 19-29.

Fry, B. 1988. Food web structure on Georges Bank from stable C, N, and S isotopic composition. Limnology and Oceanography. 33: 1182-1190.

Fry, B.; Joern, A.; Parker, P.L. 1978. Grasshopper food web analysis: use of carbon isotope ratios to examine feeding relationships among terrestrial herbivores. Ecology. 59: 498-506.

Goering, J.; Alexander, V.; Haubenstock, N. 1990. Seasonal variability of stable carbon and nitrogen isotope ratios of organisms in a north Pacific bay. Estuarine, Coastal and Shelf Science. 30: 239-260.

Hobson, K.A. 1993. Trophic relationships among high Arctic seabirds: insights from tissue-dependent stable-isotope models. Marine Ecology Progress Series. 95: 7-18.

Hobson, K.A.; Clark, R.G. 1992. Assessing avian diets using stable isotopes I: turnover of 13C in tissues. Condor. 94: 181-188.

Hobson, K.A.; Montevecci, W.A. 1991. Stable isotope determination of trophic relationships of Great Auks. Oecologia. 87: 528-531.

Hobson, K.A.; Sealy, S.G. 1991. Marine protein contributions to the diet of northern saw-whet owls on the Queen Charlotte Islands: a stable-isotope approach. Auk. 108: 437-440.

Hunt, L.E. 1993. Diet and habitat use of nesting Prairie Falcons (*Falco mexicanus*) in an agricultural landscape in southern Alberta. Edmonton, Alberta, Canada: University of Alberta. M.S. thesis.

Kemp, D.J.; Rogers, G.E. 1972. Characterization of feather and scale proteins. Biochemistry. 11: 969-975.

Knight, R.L.; Erickson, A.W. 1977. Ecological notes on Long-eared and Great Horned Owls along the Columbia River. Murrelet. 58: 2-6.

Marti, C.D. 1974. Feeding ecology of four sympatric owls. Condor. 76: 45-61.

Meng, H.K. 1959. Food habits of nesting Cooper's Hawks and Goshawks in New York and Pennsylvania. Wilson Bulletin. 71: 169-174.

Mermann, T.J.; Buehler, D.A.; Fraser, J.D.; Seegar, J.K.D. 1992. Assessing bias in studies of Bald Eagle food habits. Journal of Wildlife Management. 56: 73-78.

Minagawa, M.; Wada, E. 1984. Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between ^{15}N and animal age. Geochimica Cosmochimica Acta. 48: 1135-1140.

Mizutani, H.; Fukuda, M.; Kabaya, Y.; Wada, E. 1990. Carbon isotope ratio of feathers reveals feeding behavior of cormorants. Auk. 107: 400-403.

Mizutani, H.; Wada, E. 1988. Isotope ratios in seabird rookeries and the ecological implications. Ecology. 69: 340-349.

Mizutani, H.; Hasegawa, H.; Wada, E. 1986. High nitrogen isotope ratio for soils of seabird rookeries. Biogeochemistry. 2: 221-247.

Orians, G.; Kuhlman, F. 1956. Red-tailed Hawk and Horned Owl populations in Wisconsin. Condor. 58: 371-385.

Owens, N.J.P. 1987. Natural variations in the ^{15}N in the marine environment. Advances in Marine Biology. 24: 389-451.

Park, R.; Epstein, S. 1960. Carbon isotope fractionation during photosynthesis. Geochimica Cosmochimica Acta. 21: 110-126.

Peterson, B.J.; Fry, B. 1987. Stable isotopes in ecosystem studies. Annual Review of Ecology and Systematics. 18: 293-320.

Quinn, M.S. 1991. Nest site and prey of a pair of Sharp-shinned Hawks in Alberta. Journal of Raptor Research. 25: 18-19.

Reed, H.A.; Woods, E.F. 1964. Heterogeneity of feather proteins. Biochemical Journal. 92: 12-18.

Roth, D.; Powers, L.R. 1979. Comparative feeding and roosting habits of three sympatric owls in southwestern Idaho. Murrelet. 60: 12-15.

Schoeninger, M.J.; DeNiro, M.J. 1984. Nitrogen and carbon isotopic composition of bone collagen from marine and terrestrial animals. Geochimica Cosmochimica Acta. 48: 625-639.

Sherrod, S.K. 1978. Diets of North American Falconiformes. Journal of Raptor Research. 12: 49-121.

Taylor, D. 1984. Winter food habits of two sympatric owl species. Murrelet. 65: 48-49.

Thomsen, L. 1971. Behavior and ecology of Burrowing Owls on the Oakland Municipal Airport. Condor. 73: 177-192.

Thompson, D.R.; Furness, R.W. 1995. Stable-isotope ratios of carbon and nitrogen in feathers indicate seasonal dietary shifts in Northern Fulmars. Auk. 112: 493-498.

Wada, E.; Terazaki, M.; Kabaya, Y.; Nemoto, T. 1987. ^{15}N and ^{13}C abundances in the Antarctic Ocean with emphasis on the biogeographical structure of the food web. Deep-Sea Research. 34: 829-841.

Weir, D.; Hanson, A. 1989. Food habits of Great Horned Owls, *Bubo virginianus*, in the northern taiga of the Yukon Territory and Alaska. Canadian Field-Naturalist. 103: 12-17.

Wickman, F.E. 1952. Variations in the relative abundance of the carbon isotopes in plants. Geochimica Cosmochimica Acta. 2: 636-639.

Sex-biased Dispersal of Young Western Screech-owls (*Otus kennicottii*) in Southwestern Idaho

Ethan Ellsworth and James R. Belthoff[1]

Abstract.—We examined dispersal distance of young Western Screech-owls (*Otus kennicottii*) from nest sites to overwintering sites in relation to two hypotheses for sex-biased dispersal. Overall, young Screech-owls (N = 31) dispersed an average of 10.6 ± 1.8 km to overwintering sites, and females (14.7 ± 2.5 km; N = 13) dispersed farther than males (5.1 ± 2.3 km; N = 15). This result is not consistent with the behavioral dominance hypothesis, which predicts that individuals of the more dominant sex class (apparently females in Western Screech-owls) should be more philopatric. The mating system hypothesis, which predicts that the sex that establishes the territory should disperse shorter distances, remains tenable as an explanation for female-biased dispersal in Western Screech-owls.

Among the curious features of avian dispersal is that it is often gender biased; that is, females usually disperse more frequently or farther than males (Gauthreaux 1978, Greenwood 1980). The causes of differential dispersal are not well understood (Pusey 1987), but hypotheses that attempt to explain this pattern are common (Johnson and Gaines 1990). Two such hypotheses are (1) the behavioral dominance hypothesis (Gauthreaux 1978), which predicts that individuals of the dominant sex class force subordinates to disperse farther, and (2) the mating system hypothesis (Greenwood 1980), which argues that selection has favored philopatry among individuals of the sex that defends resources (e.g., territories) and that inbreeding avoidance causes greater dispersal of the sex being attracted. For most species of birds the two hypotheses make identical predictions. Because males typically defend territories, and males are generally dominant to females, both hypotheses predict female-biased dispersal in these species. However, the two hypotheses can be distinguished by examining a species in which males establish and defend territories but in which typical dominance patterns are reversed, so that females dominate males. In this case, the hypotheses make contrasting predictions, and the relative importance of dominance patterns and mating systems in leading to sex-biased dispersal patterns can be assessed.

The Western Screech-owl (*Otus kennicottii*) is one species of bird that appears to fit these criteria. Males select and defend territories, but pat-terns of size dimorphism are reversed from the typical pattern in passerines, for example, so that female Screech-owls are larger than males (Dimorphism Index = 2.3; Johnsgard 1988). Size is often an important predictor of domin-ance status in raptors that display reversed sexual dimorphism, including owls (Boxall 1979, Evans 1980, Keith 1964, Mueller 1986). Moreover, in an earlier study we found that the most dominant Western Screech-owl nestlings tended to be larger than their subordinate siblings, and females tended to weigh more than males (Ellsworth and Belthoff, in prep.). Thus, it is probably safe to assume that the large size of female Western Screech-owls confers upon them a competitive advantage over smaller males. Under this scenario, the behavioral dominance hypothesis predicts that females will outcompete subordinate males for available resources and effectively force males to disperse farther from the natal area. Domin-ant females also may aggressively chase less dominant males from the natal area. Either way, this contrasts with the mating system hypothesis which predicts that male Western Screech-owls, which establish and defend territories, should be more philopatric than females.

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In this study, we examined the dispersal behavior of young Western Screech-owls in relation to the behavioral dominance and mating system hypotheses. The distance of dispersal was measured from the natal area to the apparent overwintering site acquired by the dispersing young; thus, dispersal distances reported here do not represent natal dispersal distances (i.e., distance from natal to first breeding site). However, these initial movements are important in the lives of young Western Screech-owls because they represent a significant component of the dispersal process, and settlement opportunities likely decline later in the year when suitable habitats become saturated with dispersers. Furthermore, the initial stage of dispersal may be representative of final dispersal because at least some juveniles breed in the same areas in which they settled to overwinter (see Belthoff and Ritchison 1989), and adults breed in the same area in which they winter, (i.e., they are territorial residents throughout the entire year).

METHODS

Study Area

The study area included a 53 km stretch of the Snake River in Elmore and Owyhee Counties in southwestern Idaho, which included part of the Snake River Birds of Prey National Conservation Area and encompassed C.J. Strike Reservoir and portions of the Bruneau River. Here, the Snake River has carved a canyon of up to 125 m high. Above the canyon on the Snake River Plain, vegetation is characteristic of a shrub-steppe desert, and trees are largely absent. Below the canyon rim the river meanders beneath vertical volcanic cliffs and through wide terraces of the old river bed and ancient lakes. Native cottonwoods (*Populus balsamifera*), willows (*Salix* spp.), and introduced Russian olives (*Eleaegnus angustifolia*), black locusts (*Robinia pseudoacacia*), and boxelders (*Acer negundo*) grow along the Snake and Bruneau rivers in seeps and tributaries, and near farms. In these riparian habitats and woodlots, Western Screech-owls nest in natural cavities or in wooden nest boxes erected by the Bureau of Land Management.

Transmitter Application and Monitoring

Approximately 1 week prior to fledging, Western Screech-owl nestlings were fitted with radio-transmitters (Model SOPB 2190; Wildlife Materials, Carbondale, IL) and provided with a uniquely numbered aluminum leg band. At this time, we also collected blood from young with microhematicrit tubes following venipuncture of the alar vein with a microlancet, and stored the blood at -20°C until gender analyses were performed. Gender of young owls was subsequently determined by a commercial laboratory (Zoogen, Inc., Davis, CA) using DNA isolated from these blood samples.

We captured and affixed radio-transmitters to all juvenile Western Screech-owls (N = 48) in 15 families, with the exception of two juveniles that fledged before we could attach transmitters (one from Delta and one from Harris). The mean date that young left the nest box was 18 May (N = 50), ranging from 8 May to 4 June. Following fledging we located the diurnal roost sites of all radio-tagged young until they dispersed. Eight young died on the natal area before dispersing. Seven others disappeared early in the post-fledging period weeks before they should have dispersed and were assumed to be dead. Thus, we were able to monitor 35 young from fledging until dispersal. The number of days these young spent on the natal area ranged from 41-97 days (mean = 60.0 ± 2.36 [SE]), while the average dispersal date was 16 July (range: 25 June - 25 August).

To locate dispersing young, we conducted airplane searches within and outside of the boundaries of the study area. After each flight, we searched several times on the ground for juveniles located from the air. In 1994 and 1995, the initial searches were conducted on 12 July and 26 July, respectively. Subsequent aerial searches (29 August and 21 October 1994, and 13 September 1995) were conducted to locate later dispersers and track juveniles as they settled into overwintering sites. Young were relocated from the ground periodically throughout the fall until mid-November, and the last place (within an approximately 100 m radius) that young were located was considered to be their dispersal site. We considered young to be settled if they occupied a single site for at least 3 consecutive weeks, or if they changed sites early in the dispersal period but were located again in late autumn at a time when most other young had apparently settled.

Statistical Analyses

Using analyses of variance (ANOVA), we examined the effect of sex on dispersal distance of young by comparing the distance that males and females traveled from their natal area to apparent overwintering sites. Because young within a brood may not disperse independently of one another, we performed an additional analysis while blocking by brood. This analysis included only young from mixed-sex broods and for young which were located on dispersal areas (N = 6 broods).

RESULTS

We located 31 of 35 (88.6 percent) young that survived the postfledging period after they dispersed. Twenty-eight young were considered to be settled in a dispersal area because they occupied a particular site for a minimum of 3 weeks (N = 25), or were found late in the autumn at a time in which other young were apparently settled (N = 3). Considering all individuals, the average dispersal distance was 10.6 ± 1.8 (SE) km (range: 0.7-36.1; N = 31; table 1) from the nest site to the last place young were located 4-12 weeks after disper-sal. All analyses based on these data indicate that females dispersed farther than males. For example, among settled young (N = 28), females (14.7 ± 2.5 km; N = 13) were located farther from the nest than males (5.1 ± 2.3 km; N = 15; fig. 1), and the difference between the sexes was significant ($F_{1,26}$ = 7.95, p = 0.009). When only juveniles from mixed-sex broods (N = 19 owls from six broods) were considered (i.e., so that blocking by family could be accomplished to remove inter-family differences from the analysis), the average dispersal distance in females (16.4 ± 3.0, N = 10) also was greater than for males (6.0 ± 3.1, N = 9), although the difference was significant at a slightly higher alpha value ($F_{1,12}$ = 4.28, p = 0.06) than when all juveniles were considered. Finally, three young were located only once from an airplane by their transmitter signal, so their overwintering sites were not confirmed. Nonetheless, even among these "unknown" birds, females (N = 2) were farther from their natal areas the only time they were located (27.6 and 18.8 km) than was the single male (14.7 km; table 1), which is consistent with the results from young that were known or presumed to have settled and the conclusion that females of this species disperse farther than males.

DISCUSSION

Our results suggest that young female Western Screech-owls dispersed farther than males, which is consistent with the general pattern of female-biased dispersal in birds (Greenwood and Harvey 1982). It is important to note that the dispersal distances reported here for young Western Screech-owls (with one exception) are based on distances between natal and overwintering sites rather than between natal and first breeding sites. We were unable to locate the first breeding sites for most owls in the study because the radio-transmitters could not be designed to function long enough. Nonetheless, the information we obtained is valuable because it suggests that differences in distances moved by young males and females during the dispersal process may be established long before the breeding season arrives.

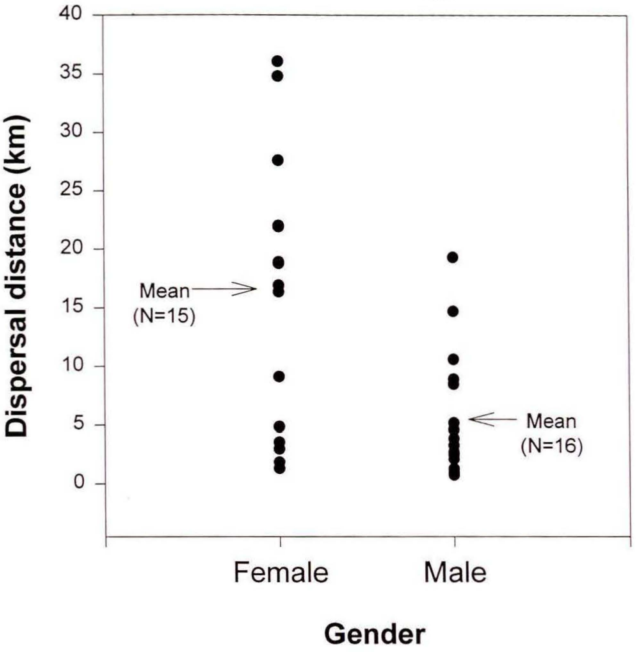

Figure 1.—*Dispersal distances from the natal area to apparent overwintering sites of female (N = 15) and male (N = 16) Western Screech-owls in southwestern Idaho in 1994 and 1995.*

If our assumption concerning patterns of dominance between sex classes in Western Screech-owls is correct, and because females dispersed farther than males, the behavioral dominance hypothesis does not appear to explain the patterns of sex-biased dispersal among Western Screech-owls in our study. Instead, the results are more consistent with the mating system hypothesis which predicts that males are more philopatric than females in

Table 1.—*Dispersal distances from the natal area to apparent overwintering sites of young Western Screech-owls (N=31) in southwestern Idaho in 1994 and 1995. A settled fate indicates that young were apparently settled in one area, as they were either located more than once or were located late in the autumn at a time when most other young were settled. An unknown fate indicates that young were only located once in a dispersal area.*

Family	Bird *Number*	Sex	Distance *km*	Fate
1994				
Cabin	103	male	4.6	Settled
	104	female	36.1	Settled
	105	female	18.8	Unknown
	106	female	4.9	Settled
	107	female	16.9	Settled
Bruneau Marsh	108	male	0.7	Settled
	109	female	3.0	Settled
	110	male	2.7	Settled[a]
	111	male	8.5	Settled
Rabbit Springs	112	female	16.4	Settled
	113	female	1.3	Nesting[b]
Trueblood	128	male	3.3	Settled
	130	male	3.9	Settled
	131	male	2.7	Settled
Boat Launch	100	male	0.9	Settled
	120	male	10.6	Settled
Treeline	136	female	27.6	Unknown
1995				
Cellar Hole	154	female	21.9	Settled
	156	female	18.9	Settled
	157	male	19.3	Settled
Upper Cabin	167	male	2.1	Settled
	170	male	14.7	Unknown
Cabin	172	female	22.0	Settled
	173	male	1.3	Settled
	174	male	5.2	Settled
Trueblood	159	male	2.5	Settled
	160	female	1.9	Settled
	171	female	3.6	Settled
CJ Strike	164	female	34.8	Settled[a]
	165	male	8.9	Settled[c]
Harris	498	female	9.1	Settled

[a] Considered to be settled because young were located in late fall at a time in which other young were settled

[b] Bred as 1-year-old.

[c] Apparently killed by a car in mid-October.

monogamous species and in which males defend territories (Greenwood 1980), like Western Screech-owls. Greenwood (1980) suggests that in these species males establish territories before females begin selecting a mate. Consequently, males settle closer to home in familiar habitat, while females do not have the costly constraint of establishing a territory. Instead, they have the capacity to choose among the available males and their territories, and females may settle farther away to avoid inbreeding (Greenwood 1980).

Although our results are more consistent with the mating system hypothesis than with the behavioral dominance hypothesis, female-biased dispersal in Western Screech-owls could be explained by factors we did not consider.

For example, sex-biased dispersal patterns may result from differential territory turnover for males and females (Waser 1985, Plissner and Gowaty 1996). That is, if one sex class vacates, through mortality or other factors, territories more frequently than the other, settlement opportunities would differ for dispersing males and females, and sex-biased dispersal patterns could result regardless of the particular mating system (Tonkyn and Plissner 1991). Unfortunately, we do not have sufficient demographic data from Western Screech-owls in our study area to evaluate this alternative hypothesis at this time.

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LITERATURE CITED

Belthoff, J.R.; Ritchison, G. 1989. Natal dispersal of Eastern Screech-owls. Condor. 91: 254-265.

Boxall, P.C. 1979. Aspects of the behavioral ecology of wintering Snowy Owls (*Nyctea scandiaca*). Calgary, Canada: University of Calgary. M.S. thesis.

Evans, D.L. 1980. Vocalizations and territorial behavior of wintering Snowy Owls. American Birds. 34: 748-749.

Gauthreaux, S.A., Jr. 1978. The ecological significance of behavioral dominance. In: Bateson, P.P.G.; Klopfer, P.H., eds. Perspectives in ethology. vol 3. New York: Plenum Press. 177-254 p.

Greenwood, P.J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Animal Behaviour. 28: 1140-1162.

Greenwood, P.J.; Harvey, P.H. 1982. The natal and breeding dispersal of birds. Annual Review of Ecology and Systematics. 13: 1-21.

Johnsgard, P.A. 1988. North American owls, biology and natural history. Washington DC: Smithsonian Institute Press. 295 p.

Johnson, M.L.; Gaines, M.S. 1990. Evolution of dispersal: theoretical models and empirical tests using birds and mammals. Annual Review of Ecology and Systematics. 21: 449-480.

Keith, L.B. 1964. Territoriality among wintering Snowy Owls. Canadian Field-Naturalist. 78: 17-24.

Mueller, H.C. 1986. The evolution of reversed sexual dimorphism in owls: an empirical analysis of possible selective factors. Wilson Bulletin. 98: 387-406.

Plissner, J.H.; Gowaty, P.A. 1996. Patterns of natal dispersal, turnover and dispersal costs in Eastern Bluebirds. Animal Behaviour. 51: 1307-1322.

Pusey, A.E. 1987. Sex-biased dispersal and inbreeding avoidance of birds and mammals. Trends in Ecology and Evolution. 2: 295-299.

Tonkyn, D.W.; Plissner, J.H. 1991. Models of multiple dispersers from the nest: predictions and inference. Ecology. 72: 1721-1730.

Waser, P.M. 1985. Does competition drive dispersal? Ecology. 66: 1171-1175.

Comparative Study of General Public Owl Knowledge in Costa Rica, Central America and Malawi, Africa

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Abstract.—The public knowledge of owls in Central America and Africa was compared based on 162 interviews in Costa Rica and 147 in Malawi. General knowledge of owls included: species, common names, habitats, food, and calls, and was quite similar in both study areas. In Malawi, more than 90 percent of the respondents connected owls with bad luck, witchcraft, and death. In Costa Rica, only 4 percent associated owls with bad omens and 3 percent listed them as frightening. Strong negative superstitions about owls are contributing to the unnecessary killing of owls in Africa, but they are also killed in Central America. Further education of the general public is needed on how beneficial owls are, and that the superstitious beliefs and myths about them are groundless.

The survival of several kinds of living creatures, including reptiles, bats, and owls, depends not only on environmental issues but also on social and cultural matters. The value of people's participation in resolving complex conservation issues has been rediscovered only lately (Raval 1994).

It is highly likely that owls were among the first birds to be noticed by ancient man, probably because their vocalizations in the night would cause havoc in the superstitious mind (Freethy 1992).

Few other birds or other animals have gathered so many different and contradictory beliefs about them: owls have been both feared and vener-ated, despised and admired, considered wise and foolish, associated with witchcraft and medicine, the weather, births and deaths—and have even found their way into *haute cuisine* (Weinstein 1989).

Folklore has it that owls are birds of ill omen and that deception is one of their favorite ploys. Conversely, owls have been widely admired through the ages by deities, scholars, poets, and animal lovers in general (Cenzato and Santopietro 1991).

Owls have a well-defined position in the folklore of every country in which they live; and they can be found everywhere with the exception of the Antarctic and a few remote islands (Leach 1992). There are 17 owl species in Costa Rica (Stiles and Skutch 1989), but only four species are common in the study villages (Enriquez 1995). Malawi has 12 different owl species, eight of which are common all over the small country (Benson and Benson 1977).

In this paper we describe and compare the cultural relationships between owls and human communities based on two interview studies undertaken by the authors in Costa Rica, Central America (Enriquez and Rangel 1996) and in Malawi, Central Africa (Mikkola 1997a).

METHODS

In Costa Rica, 162 persons were interviewed between April and September 1995, and in Malawi 147 persons between July and November 1996. The questionnaires were more or less similar although the interview language in Costa Rica was Spanish and in Malawi it was English. Sampling methods and pretesting of the interview questionnaire are described in detail in the original papers (Enriquez and Rangel 1996, Mikkola 1997a).

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Interviewed Persons

Age and sex distribution of persons interviewed in Costa Rica and Malawi was similar, although in Costa Rica middle-aged persons were not interviewed. Females comprised 46 percent of those interviewed in Costa Rica versus 37 percent in Malawi. In Costa Rica, females were 12 to 91 years old, in Malawi 11 to 72 years old. The age of interviewed males in Costa Rica varied from 12 to 95 years, and in Malawi from 10 to 82 years. In Malawi, many people (est. 50), especially women in the rural areas, refused to answer the questions, explaining why the Malawian material is more male biased than that from Costa Rica.

RESULTS

Common Local Owl Names

In Costa Rica, we recorded 21 popular or local names, but "Cara de Gato" (Cat face) and Oropopo (onomatopoetic) were the most common names used by the adults, while "Buho" (owl) was the name most used by adolescents and overall in Costa Rica (table 1).

In Malawi, some 40 different local names were recorded due to the numerous tribal languages in that country. Most commonly used names were: Kadzidzi, Matchichi, and Phululu. The English term "owl" was familiar to 65 percent of the interviewed persons. The meaning of local names was not always clear, in either Costa Rica or in Malawi. In Costa Rica, adults as a group knew more local owl names than younger persons, and in both Costa Rica and Malawi men knew more local names than did women.

General Owl Knowledge

Around 44 percent of the Costa Rican respondents knew only one owl, or treated all owl species as one entity. There was a great difference between the sexes, 56 percent of females knew only one owl against 35 percent of males (fig. 1).

In Malawi, 65 percent knew only one owl, and there was no difference between female and male knowledge of species (fig. 1). In Costa Rica, only 4 percent knew more than three species (out of 17 possible), while in Malawi 9 percent knew more than three species (out of 12).

Owl Habitats

Both in Costa Rica and Malawi, people correctly listed mountains and forests the most important habitats for the owls (table 2). In Malawi 17 percent listed graveyards as owl habitat, but in Costa Rica owls were not connected with graveyards at all. In Costa Rica all interviewed people lived in the villages nearby a large, protected, forest reserve with

Table 1.—*Four most common local names of owls in Costa Rica and in Malawi.*

Name	Standing for	Females	Males	Total
			Costa Rica (%)	
Buho	Owl	76	77	77
Cara de Gato	Tyto alba	37	46	41
Oropopo	Pulsatrix perspicillata	26	41	34
Hu de Leon	Ciccaba virgata	16	34	26
Total no. of answers		74	88	162
			Malawi (%)	
Kadzidzi	Owl, maybe also Bubo africanus	96	96	96
Owl	Owl	73	60	65
Matchichi	Owl, species ?	44	71	61
Phululu	Owl, species ?	53	54	54
Total no. of answers		55	92	147

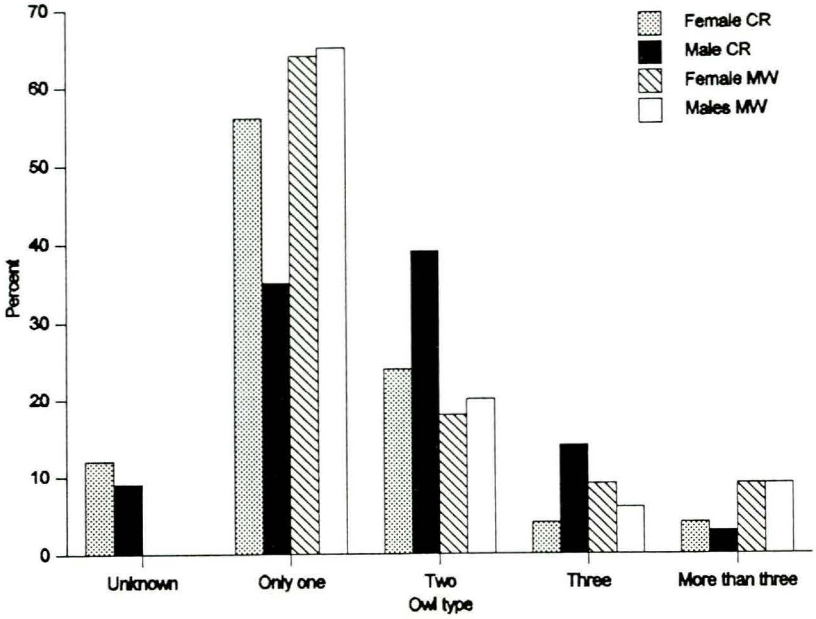

Figure 1.—*General knowledge of owl species in Costa Rica and Malawi.*

Table 2.—*General knowledge of owl habitats in Costa Rica and in Malawi.*

Habitat	Costa Rica (%) Females	Costa Rica (%) Males	Costa Rica (%) Total	Malawi (%) Females	Malawi (%) Males	Malawi (%) Total
Mountains	85	80	82	60	67	65
Forests	80	76	78	100	96	96
Wetlands	-	-	-	20	51	40
Fields	10	16	13	22	32	28
Villages	-	-	-	48	52	50
Cities	3	2	3	28	33	31
Graveyards	-	-	-	16	18	17
River banks & gullies	3	6	4	2	11	8
No. of answers	74	88	162	50	91	141

few graveyards present. Due primarily to firewood gathering, wooded areas around Malawian villages are mainly associated with graveyards.

Owl Food

In both countries, people correctly answered that owls mainly eat small mammals (table 3). In Costa Rica, insects were listed as owl prey in 13 percent of the answers; while in Malawi the corresponding value was 77 percent. In Malawi, 69 percent had reported snakes as food against 17 percent in Costa Rica.

Interestingly, both in Costa Rica and in Malawi, approximately an equal proportion of people were wrongly convinced that owls were eating fruits, but only in Malawi did people list bread and maize as owl food (table 3).

In Costa Rica, 74 percent had never seen an owl catch or eat prey, while in Malawi those seeing owls actually take prey were 38 percent. In Malawi, people saw the following prey items (n=50) eaten: rats (9), hares (3), birds (2), frogs (2), snakes (7), insects (10), mice (5), dog (1), chicken (5), lizards (5), and fish (1).

Insects, rats, and snakes were frequently observed to be eaten by owls, which was also suggested in table 3.

Table 3.—*General knowledge of owl food in Costa Rica and in Malawi.*

Food	Costa Rica (%)			Malawi (%)		
	Females	Males	Total	Females	Males	Total
Small mammals	34	48	41	50	84	72
Cats	5	11	9	-	5	3
Chicken	10	14	12	4	23	16
Other birds	12	11	12	31	45	40
Frogs	1	5	3	2	4	4
Snakes	19	16	17	63	73	69
Lizards	4	8	6	46	61	56
Worms	4	3	4	2	2	2
Fish	1	1	1	19	14	15
Insects	*12*	14	13	77	77	77
Fruits	31	14	22	10	25	20
Bread and maize	-	-	-	2	3	3
Meat	4	2	3	-	-	-
No. of answers	74	88	162	48	88	136

Owls Calling

In Costa Rica, 85 percent of those surveyed had heard owls calling at least a few times, while in Malawi the corresponding figure was 98 percent (100 percent for the males). A majority of people in Costa Rica connected the owl calls with summer and with a full moon.

In Malawi, owl calls were not linked to any season, rainy or dry, but 76 percent said that owls called at night in the forest (30 percent), near houses (28 percent), and in villages (24 percent). Graveyards were mentioned by 9 percent of the respondents.

People Killing or Sacrificing Owls

In Costa Rica, every sixth, and in Malawi, every fourth interviewed knew somebody who had killed or sacrificed an owl or owls. In Costa Rica, owls were killed because they are thought harmful (eat chickens), just for fun, for curiosity, to study, because they were 'causing' bad luck or because they were 'bigs'.

In Malawi, the reasons for 41 killings were listed as below:

- superstitious beliefs to avoid bad omen	30%
- to make magic medicine[3]	5
- because they make too much noise	13
- just for fun during the hunt	23
- to be eaten as a relish	17
- because it killed a hen	2
- because it attacked first	2
- because it entered into a hospital	2
- because it was nesting too near the house	2
- killed by a car	2
- did not know why he/she killed the owl	2
Total	100%

There seems to be no mercy for owls in Malawi, as they are commonly killed for many reasons.

Owl Beliefs

In Costa Rica, only 55 percent of those interviewed knew of beliefs or myths while in Malawi well over 90 percent knew and had strong beliefs and/or superstitions about owls.

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[3] To make magic medicine needs an explanation. In Malawi, an owl-based medicine is only used for witching and killing people and not for healing any diseases (Mikkola 1997b).

In Costa Rica, those who knew stories and myths were older people, mainly old men. In Malawi, 92 percent of the answers from young and old respondents repeated that owls were responsible for bringing bad luck to humans, foretelling death, and that owls were associated with witchcraft.

Bad luck and death-related stories were also the most common myths in Costa Rica, but only 26 percent believed in those myths, 53 percent of the believers were women. Only 13 percent of young persons had any superstitious beliefs in Costa Rica, and 62 percent of them were females. Women appear to be more superstitious than men in both countries.

Some typical myth and story statements were as follows:

"Owls are birds of bad omen and bad luck, and have some secrets because they are nocturnal, they have a bad spirit (Costa Rica)."

"Should an owl settle on a roof of a hut (house), it is regarded as a messenger of death. Even if it merely screams while flying over or near the hut (house), it is believed to be predicting some misfortune to the inhabitants (Malawi)."

"Before my wife died, one owl was calling several days and people kept telling me that someone will die soon (Costa Rica); the Malawian version being: "When people hear an owl singing they believe that someone will pass away during that night in their village."

"Owls are not real birds, as they are created by witches or wizards for bewitching people (Malawi)."

Also in Costa Rica owls were seen as messengers of a sorcerer.

In both Costa Rica and Malawi people mentioned that owls attack people and try to make them blind by grasping their eyes. Indeed, it is true that some owls get very aggressive towards any intruders when defending their fledged young or at their nest. In Europe, at least four people have lost an eye due to attacking owls (Mikkola 1983).

In Costa Rica, many people related owls with the cats, even named the Barn Owl as "Cara de Gato" (Cat face), but in Malawi only one person said there was some resemblance between an owl and a cat's head. In non-scientific terms, an owl is a cat with wings. It is a creature superbly adapted for hunting small rodents, watching silently until it pounces. Yet, like the cat, it can be noisy on occasions, rending the night with a never-ending series of raucous courting screams and hoots (Sparks and Soper 1989).

Only in Malawi was there a common belief that "if an owl crosses the road while you are traveling you are sure to get some misfortune."

Interestingly, this same belief is very common in Europe, at least in Finland, but only when a black cat crosses the road and not an owl. In Morocco, on the other hand, the hoot of an owl was merely a bad omen for any traveler about to set out on a journey (Weinstein 1989).

Owl Classification

In conclusion, the respondents were asked to classify owls according to their knowledge and beliefs (fig. 2). In Malawi, a great majority classified owls as a bad omen. Fewer Malawian women found owls beneficial than men (fig. 2). In Costa Rica, fewer males and females associated owls with a bad omen. Five percent of the women and 1 percent of the men in Costa Rica listed owls as frightening, while in Malawi, 29 percent of the females and 20 percent of the males admitted being scared or terrified even to talk about the owls. Again, both in Costa Rica and in Malawi women appear more superstitious than men (fig. 2).

A British television survey interviewed over 300 people above the age 15 about their animal likes and dislikes. When given a choice between the terms frightening and non-frightening, 39 percent of the people found owls frightening, 35 percent did not, 26 percent preferred to view owls as neither (Burton 1992).

In Costa Rica, many people, especially young persons, had obtained more knowledge on owls through television and by visiting zoos. In Malawi, there is no television, and only the City of Blantyre has a small zoo with no or a very few owls on display. Due to exposure to new knowledge about owls from TV and zoos, some young people in Costa Rica concluded that owls are clever and intelligent. In Malawi, none felt that way about owls.

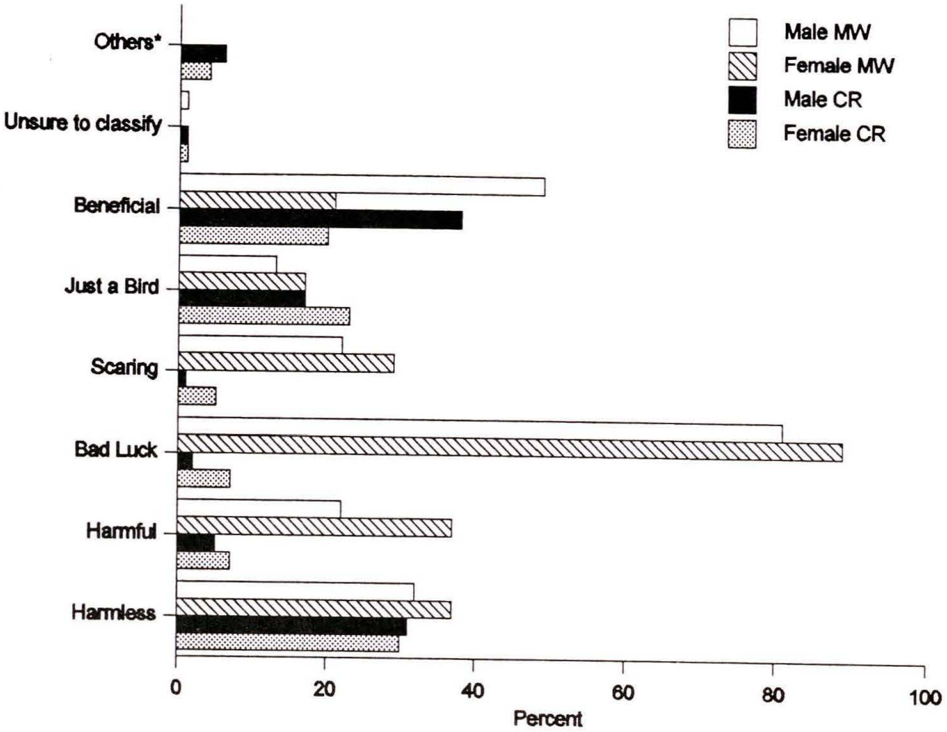

Figure 2.—*Classification of owls in Costa Rica and Malawi.*
* Including: proclaming, brave or fierce, and impressive.

DISCUSSION

Interviews in Costa Rica and Malawi confirmed that there is a widespread belief that hearing or seeing an owl is an omen of death and disaster, a conviction which possibly originates from Africa (Mikkola 1995).

In Costa Rica, a majority do not believe this superstition, but stated that old people still believe myths about owls; some admitted that owls can cause them fear and terror. In both countries women were more superstitious than men.

With the dying out of superstitions by the 20th century—in the West at least—the owl has assumed its position as a symbol of wisdom (Weinstein 1989).

In Malawi and Costa Rica, people who thought of owls as beneficial and effective controllers of agricultural pests (e.g., mice, rats, and insects) also connected owls with witchdoctors and with magic powers. One possible explanation of strong superstitions existing in the 20th century could be that in Malawi owls were often correctly associated with graveyards. Due to heavy deforestation in most Malawian villages, graveyards are the only wooded areas remaining. Owls use graveyards for breeding, calling, and daytime roosting. As a result, people are meeting owls more and more often in graveyards, thus reinforcing their strong belief that owls are connected with death.

In Malawi and Costa Rica, people had a lot of general knowledge of owls, but in many cases this knowledge was unclear or wrong. It is a paradox, that in reality owls are one of the most beneficial groups of birds, but one of the least understood (Clark *et al.* 1978).

Holl *et al.* (1995) suggest that it is important to consider how peoples' attitudes toward wildlife affects their action toward conservation of species and ecosystems. Understanding both environmental problems and the influence of human behavior is indispensable to achieve success in the conservation of owl populations around the world. Only by educating people, through schools and television, of the roles owls have in nature, will superstitious beliefs in them be overcome.

ACKNOWLEDGMENTS

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LITERATURE CITED

Benson, C.W.; Benson, F.M. 1977. The birds of Malawi. Limbe, Malawi: Montfort Press. 263 p.

Burton, J.A. 1992. Owls of the world. London, England: Peter Lowe, Eurobook Limited. 208 p.

Cenzato, E.; Santopietro, F. 1991. Owls: art, legend, history. Toronto, Canada: Little, Brown & Co. 112 p.

Clark, R.; Smith, D.W.; Kelso, L.H. 1978. Working bibliography of owls of the world. Tech. Ser. 1. Washington, DC: National Wildlife Federation. 319 p.

Enriquez, R.P. 1995. Abundancia relativa, uso de habitat y conocimiento popular de los Strigiformes en un bosque humedo tropical en Costa Rica. Heredia, Costa Rica: Universidad Nacional de Costa Rica. 81 p.

Enriquez, R.P.; Rangel, S.J. 1996. Conocimiento popular de las lechuzas en los alrededores de un bosque humedo tropical protegido. Vida Silvestre Neotropical. 5(2): in press.

Freethy, R. 1992. Owls: a guide for ornithologists. Hildenborough, England: Bishopsgate Press. 134 p.

Holl, K.D.; Daily, G.C.; Ehrlich, P.R, 1995. Knowledge and perceptions in Costa Rica regarding environment, population, and biodiversity issues. Conservation Biology. 9 (6): 1548-1558.

Leach, M. 1992. The complete owl. London, England: Chatto & Windus. 170 p.

Mikkola, H. 1983. Owls of Europe. Calton, England: T. & A.D. Poyser. 397 p.

Mikkola, H. 1995. Owls in African superstitions. Owls Magazine. 1(4): 2-3.

Mikkola, H. 1997a. General public owl knowledge in Malawi. The Journal of the Society of Malawi: in press.

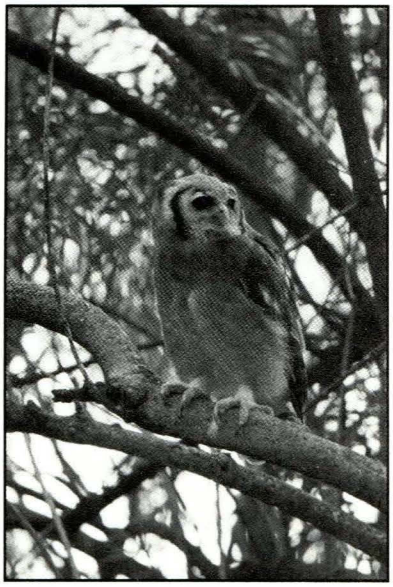
Mikkola, H. 1997b. Owls in African witchcraft. MS.

Raval, S. 1994. Wheel of life: perceptions and concerns of the resident peoples for Gir National Park in India. Society and Natural Resources. 4: 305-320.

Sparks, J.; Soper, T. 1989. Owls: their natural and unnatural history. London, England: David & Charles Publishers. 240 p.

Stiles, G.; Skutch, A. 1989. A guide to the birds of Costa Rica. Ithaca, NY: Cornell University Press. 511 p.

Weinstein, K. 1989. The owl in art, myth, and legend. New York, NY: Crescent Books. 144 p.



Hannu Hautala

Milky Eagle Owl (*Bubo lacteus*) is the largest owl in Malawi, length 66 cm (26 inches).

Autumn Populations and Movements of Migrant Northern Saw-whet Owls (*Aegolius acadicus*) at Little Suamico, Wisconsin

Tom C. Erdman, Tom O. Meyer, Jerry H. Smith, and Debra M. Erdman[1]

Abstract.—Northern Saw-whet Owls (*Aegolius acadicus*) were once considered a "rare" bird in Wisconsin. In the 1960's mist netting at bird-banding stations revealed Saw-whets to be a regular, uncommon migrant. Passive mist netting was initiated at the Little Suamico Ornithological Station in 1971. Our Saw-whet Owl experiences were similar to other banding stations until 1986, when we developed an "audiolure". This technique, utilizing an amplified Saw-whet "solicitation" courtship call increased our annual catch more than tenfold. Now in use at major banding stations in the western Great Lakes area, this technique has resulted in over 2,000 Saw-whets being netted each autumn. Currently at Little Suamico 5 percent of adult owls netted have been previously banded. Approximately 40 percent of owls netted are northbound. Direct interstation recoveries reveal that Saw-whets migrate slowly at our latitude and often not in the expected southbound direction. Adults move greater distances per night than immatures. More than 200 recoveries and recaptures in subsequent years have been generated at Little Suamico since 1986. Migration dates and nightly travel distances suggest that many of the Saw-whet Owls that we encounter spend the winter in Wisconsin.

Today more Northern Saw-whet Owls (*Aegolius acadicus*) are banded each year in North America than any other owl species. Bird-banding stations in the western Great Lakes region capture several thousand annually, mainly during autumn migration. Two major "breakthroughs" in capturing these owls have greatly facilitated these efforts. The first came from the Cedar Grove Ornithological Station located in southern Wisconsin along Lake Michigan. Mueller and Berger (1967) were the first to report that "numbers" of these owls could be captured in autumn migration with the use of mist nets left open at night. Passive mist netting has been in use at numerous bird-banding stations since the 1960's with varying degrees of success depending upon location. The second significant breakthrough was developed at the Little Suamico Ornithological Station (LSOS) in northeastern Wisconsin. In 1986 we developed an audiolure technique, utilizing an amplified Saw-whet "solicitation" courtship call. This technique allowed us to reduce the number of nets in use by over 50 percent while increasing captures tenfold. Since 1986, over 6,000 Saw-whet Owls have been captured at LSOS and two nearby substations. Subsequently, we obtained additional encounter data on close to 400 owls. In this paper we examine some direct interstation recoveries in terms of nightly movements and habitat.

STUDY AREA AND METHODS

The Little Suamico Ornithological Station is located along the west shore of Green Bay, approximately 17 kilometers north of the city of Green Bay at 44°40' N and 87°50' W. The bayshore topography is flat, gently sloping upward to the west. The difference in elevation is so slight between the station and the bay, that during periodic episodes of high water levels, wind driven seiches have flooded the station area.

Extensive marsh, shrub swamp, and deciduous swamp forest lie to the northeast, east, and south. The adjacent land to the west and north consists of dairy farms and old fields intermixed with woodlots. Farther north and northwest, continuous forest becomes predominant. Little Suamico Ornithological Station is near the southern edge of the continuous forest. South of Green Bay the habitat changes to primarily open agricultural land with scattered small woodlots. A more detailed description of LSOS can be found in Brinker and Erdman (1983) and the vegetation of the region in Robbins (1991).

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Passive netting for owls was initiated in 1971 when LSOS was founded. Although the site was picked primarily for diurnal raptor migration, it was assumed that nocturnal migrants—owls—would also be captured. Beginning in 1972 attempts were made to locate local owl flight lanes. In general, a net placed anywhere in the area eventually yielded owls. The number of nets monitored increased annually until 1978, when our effort peaked with 38, 12-m, 61-mm mesh nets, stacked two high. Approximately 0.5 kilometer of nets scattered throughout the area took about 2 hours to check. A then station record of 141 owls were netted in 1978, of which 108 were Saw-whets. While the increased number of nets and work produced more owls, the drain on human and financial resources was great.

In an effort to ascertain our degree of success at capturing owls migrating through the area, we transported a total of 150 owls 1.6 km to the northeast during the next several autumns to see how many would be recaptured. Much to our dismay, only four (2.7 percent) of these birds were subsequently renetted in the same season. We speculated that either the owls were able to avoid being netted again, which seemed unlikely since they would only have knowledge of the location of the nets they'd previously been caught in, or if we were netting only a very small portion of owls moving through the area.

This question was resolved in 1986. Since the mid-1970's attempts to lure owls to the nets were made by placing captive bait animals, feral Pigeons (*Columba livia*), Starlings (*Sturnus vulgaris*), gerbils (*Meriones unguiculatus*), and mice (*Peromyscus leucopus*) in cages or bal-chatri's near the nets. We also attempted to entice them by using amplified taped distress calls of passerines and electronic "chirping" Christmas tree bird ornaments. These efforts had very limited success and generally only worked on the larger owls—mainly Long-eared (*Asio otus*) and Barred Owls (*Strix varia*).

The extremely high water levels in 1986 left LSOS in a sorry and soggy state. One-third of our normal 100-day operation found us totally under water; the high water made it impossible for us to run our outlying net lines, for these areas were often submerged under up to 1-m of water. Only 13 nets around the hawk trapping area and station could be safely run. We literally spent the entire trapping season in hip boots and waders. However, the high water did leave time for additional experimentation with owl audiolures. As of 22 October 1986 only 30 Saw-whets had been netted. On 23 October the "primary" or "solicitation" call of a Saw-whet was played for the first time, and resulted in 12 Saw-whets netted in the first hour of operation. It appeared *the* lure had been found. Not only were we netting greater numbers of Saw-whets, but many more could be heard calling from surrounding trees. Unfortunately it was late October and the main flight had already passed; but not before we caught 132 Saw-whets. We have continued to use the audiolure ever since.

Since 1987, we have standardized our amplified audiolure to produce a sound pressure level of 100-110 decibels. On a calm night we can hear this tape 1.5 km away. The primary solicitation call of a Northern Saw-whet Owl is recorded on a 3 minute continuous loop cassette tape. Complete details and a schematic can be found in Erdman and Brinker (1997) in this proceedings.

Captured owls were temporarily held in individual holding boxes until processed and banded. Owls were aged based on plumage characteristics, measured and weighed. Net capture location, direction, and net deck (height) were also recorded for each owl. Owls netted in early morning were held until the following evening for release.

A summary of our banding records was obtained from the Bird Banding Laboratory, U.S.G.S. Biological Resources Division. Only verified direct recoveries from and to other banding stations in the same autumn were used in our analyses (tables 1, 2, and 3). These include Wisconsin stations located to the south of LSOS; Cedar Grove Ornithological Station (D. Berger), Woodland Dunes Nature

Center (B. Brouchoud), and to the west southwest; Pulaski (M. Wierzbicki), and Linwood Springs Research Station (E. Jacobs). A single station record outside of Wisconsin came from the southeast at Halifax, NC (F. Enders). Stations to the northwest, north and northeast of LSOS are: Hawk Ridge, Duluth, MN (D. Evans), Cape Thunder, Ont. and Whitefish Point Bird Observatory, Paradise, MI. Owl movements between LSOS and/or substations at Pensaukee and Lena were not included in this analysis.

RESULTS

The effectiveness of the audiolure in attracting Saw-whet Owls for capture was dramatic (fig. 1). The annual mean number of owls captured in the years of passive net use was 57 (range 15-108). With the use of the audiolure the mean number exceeded 600 owls, over a tenfold increase.

Over 40 percent of the Saw-whets netted at Little Suamico were northbound. Most were captured low in the nets, with 60 percent recorded within 1.7 m and 95 percent within 3.4 m of the ground. Over 90 percent of those recaptured at Little Suamico in the same season were netted in a higher deck (level) than their initial capture.

Ten to 15 percent of the Saw-whet Owls captured with the use of the audiolure weighed more than 100 g. Owls exceeding 100 g comprised only 1 percent of the birds netted passively. Further, an increased mass of almost 3 g was recorded for owls captured using the audiolure. An increased mass was also recorded for almost all of the owls recaptured more than 24 hours after release.

Analysis of 99 direct recoveries of owls banded at LSOS and recaptured at other stations in the same season are presented in table 1. A total of 85 owls (86 percent) comprised of 48 adults and 37 juveniles, were recaptured to the south and southeast. Another 14 owls (14 percent) evenly split between adults and juveniles, were recaptured to the west and southwest.

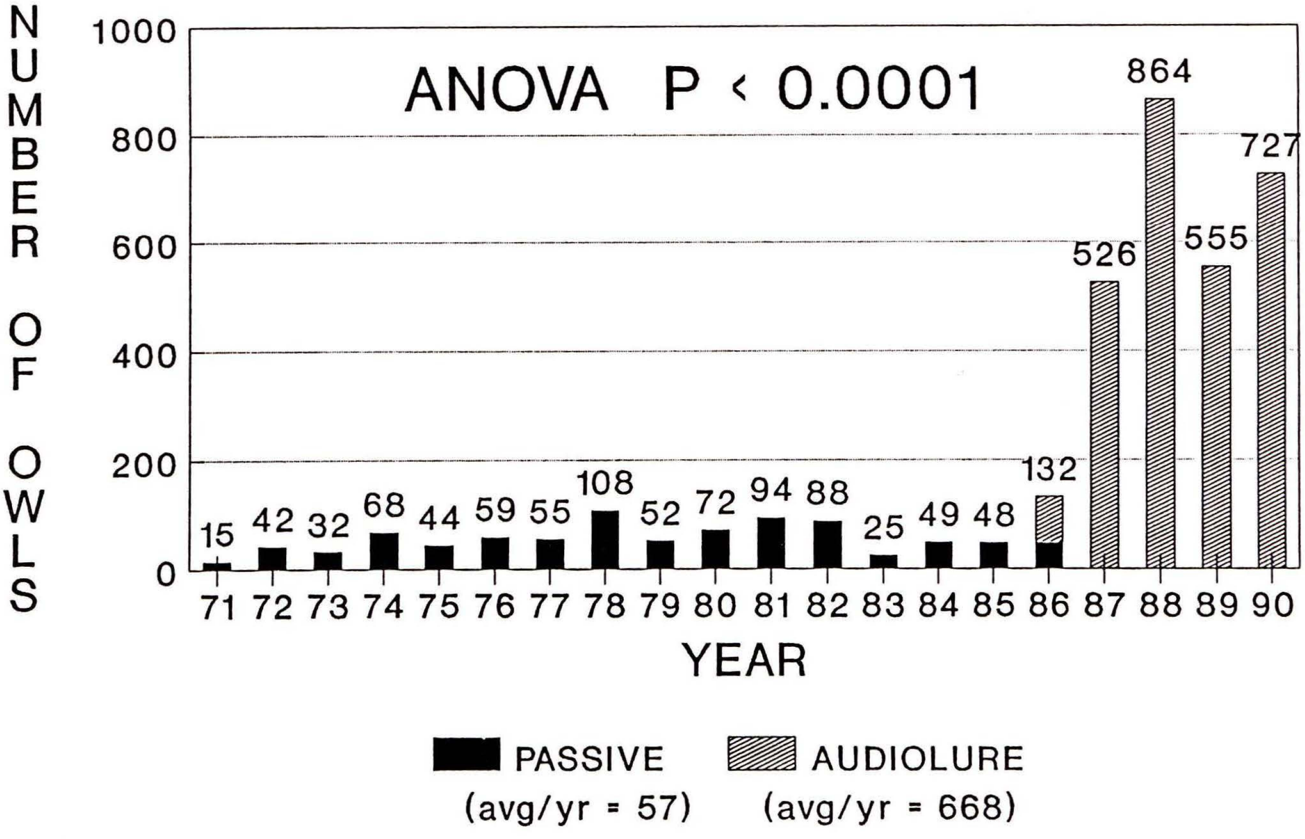

Figure 1.—*Number of Northern Saw-whet Owls captured, Little Suamico Ornithological Station, Wisconsin.*

Nightly movements of these owls averaged 7.7 km (range 1.0-44.8 km). Adults were more mobile, averaging 8.3 km, (range 2.6-44.8 km) nightly, 20 percent more than average juvenile nightly progress of 6.9 km (range 1.0-22.4 km). One long distance movement of 1,344 km by a juvenile owl in 1995 from LSOS to Halifax, NC, revealed an average nightly movement of 32 km.

At LSOS we captured 6 owls (4 adults and 2 juveniles) which had been banded north of Wisconsin earlier the same season (table 2). Average nightly movements of four adults from Hawk Ridge, Duluth, was 29.6 km (range 18.2-80 km). A juvenile from Whitefish Point B.O., MI averaged 28 km per night. Another juvenile originally banded at Cape Thunder Ont., averaged either 33.3 km or 21.8 km nightly, depending upon whether the owl crossed Lake Superior or traveled along the north shore and passed Duluth.

DISCUSSION

Prior to 1986, our experiences with Saw-whet Owls paralleled those of most other owl banding stations. For example: owls were most often netted on the leeward side of the woods on windy nights and owls were seldom netted on clear nights during a full moon. This has changed with the use of the audiolure technique. Owls are netted regardless of wind direction at LSOS. Wind velocity does affect the distance the audiolure can be heard. In October 1987, our best results came on a clear night with a full moon when 85 Saw-whets and one Long-eared Owl were captured. Saw-whet Owl migration peaks at our latitude usually in the second or third week of October. Typically, during this peak there will be one night when we net 10 percent of the years' total. This was true while passive netting and continues with the use of the audiolure.

The increase in mass of owls netted with the audiolure and the higher percentage of individuals exceeding 100 grams, suggests that we are now sampling more of the population or a different subpopulation (females?). We suspect that in the past, more of the owls we netted passively were hunting, while owls lured in by the call may have already fed and are migrating. They are also responding to a different stimulus.

That 40 percent of the owls netted at LSOS using the audiolure were northbound, moving opposite the expected migrational direction, is still puzzling. Initially we believed that these owls had passed higher overhead or were lured in from some distance to the east or west of the station. Since establishing two substations (Pensaukee and Lena) north of LSOS we have verified that some owls are indeed moving northward in autumn. We captured 11 owls (10 adults and a juvenile) in the same autumn that they were originally trapped and marked at the four banding stations located to the south and west of LSOS in Wisconsin. One adult from Cedar Grove traveled 136 km north in 12 nights, an average of 11.3 km per night. The origins of these northbound owls is still speculative. They could be dispersing individuals from the Wisconsin breeding population. Typically, juvenile raptors are more likely to disperse in random directions. That 10 of the 11 previously marked owls we captured moving north were adults suggests that this may not be the situation. These could also be owls from some distance north of Wisconsin which, having reached the southern limits of their autumn migration are now searching for suitable wintering habitat with adequate prey resources.

The banding stations at LSOS, Pulaski, and Linwood Springs are all located near the southern edge of the continuous northern forest in Wisconsin. Both the Woodland Dunes and Cedar Grove stations are located over 80 km south of this forest edge, and owls must cross open agricultural land with small scattered woodlots to reach them.

The comparison of long (> 320 km) and short (< 160 km) owl movements indicate either a change in owl migratory behavior and/or motivation (table 3). Owls moving south across the forested area of northern Wisconsin moved at an average nightly rate of 28 to 30 km. One adult moved from Hawk Ridge, Duluth to LSOS in only 5 nights, averaging 80 km per night. Owls moving south and west from LSOS averaged 7.7 km per night (range 1-50 km), which is roughly only 25 percent of the distance covered nightly by owls arriving at LSOS from the north. Perhaps the migratory behavior of owls varies dependent upon the habitat or prey resources encountered. Does it take an owl longer to traverse an open area of fragmented forests than an area of continuous forest?

Table 1.—*Autumn Northern Saw-Whet Owl movements in Wisconsin—direct recoveries from Little Suamico Ornithological Station, Wisconsin.*

Study area	Owls		Average number of nights	Range	Average km/night	Range
				Number nights		*(km/night)*
Cedar Grove O.S.	Total	61	15.7	3-37	9.17	3.68-44.8
170°S	Juv.	26	16	6-37	8.58	3.68-22.4
85 miles/136 km	Adult	35	14.7	3-30	9.63	4.48-44.8
Woodland Dunes Nature Center	Total	23	15.6	5-30	5.29	2.72-16.64
155°SSE	Juv.	10	15.2	5-30	5.47	2.72-16.64
52 miles/83.2 km	Adult	13	16	7-28	5.16	2.96-11.85
Pulaski	Total	6	12.2	2-22	1.6	.96-10-4
260°WSW	Juv.	5	13.0	2-22	1.6	.96-10.4
13 miles/20.8 km	Adult	1	8.0	8	2.56	2.56
Linwood Springs Research Station	Total	8	20.2	12-27	7.68	5.6-12.64
260°WSW	Juv.	2	26	12-27	5.84	5.6-6.08
95 miles/140 km	Adult	6	18.3	12-26	8.30	5.4-12.64

Table 2.—*Northern Saw-whet Owl—autumn distance movements to and from Little Suamico Ornithological Station, Wisconsin.*

Study area	Owls		Average number of nights	Range	Average km/night	Range
				Number nights		*(km/night)*
Hawk Ridge, Duluth **to Little Suamico** 250 miles/400 km	Adults	4	13.5	5-22	29.6	18.24-80
Cape Thunder, Ont. **to Little Suamico** 285 miles/456 km (crossing Lake Superior)	Juv.	1	21	21	21.76	21.76
438 miles/700 km (passing Duluth)	Juv.	1	21	21	33.28	33.28
Whitefish Point B.O. **to Little Suamico** 210 miles/336 km	Juv.	1	12	12	28	28
Little Suamico **to Halifax, NC** 840 miles/1,344 km	Juv.	1	41	41	32	32

Table 3.—*Comparison of long and short distance autumn movements of Northern Saw-whet Owls at Little Suamico Ornithological Station, Wisconsin..*

Distances traveled	Owls		Average distance	Range
	Number		*km/night*	*km/night*
Short Distance	Total	98	7.69	.96-44.8
< 100 miles/160 km	Juv.	43	6.92	.96-22.4
	Adults	55	8.30	2.56-44.8
Long Distance	Total	7	[1]30.30 or 28.7	18.24-80
> 200 miles/320 km	Juv.	3	[1]31.36 or 27.52	21.76-33.28
	Adults	4	29.6	17.6-80

[1] Cape Thunder owl calculated as crossing Lake Superior or passing through Duluth.

Although sample sizes are small, there appears to be no difference in average nightly movement rates between adult and juvenile owls documented in long distance(> 320 km) movements. All but one of these arrived at LSOS from the north passing over or through continuous forest. Short distance (< 160 km) movement rates of owls moving south of LSOS reveal that adults traveled an average of 20 percent farther each night than the juveniles (table 3). These owls are passing through much more diverse habitats.

The long distance movement of a juvenile Saw-whet Owl to Halifax, NC in 1995 which averaged 32 km per night indicates that some owls move at rates similar to those reaching LSOS from the north (table 3). Perhaps the more northern populations of Saw-whets are more migratory.

We suspect, based on low nightly movement rates, that many Northern Saw-whet Owls encountered at LSOS winter in Wisconsin.

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LTERATURE CITED

Brinker, D.F.; Erdman, T.C. 1983. Characteristics of autumn Red-tailed Hawk migration through Wisconsin. In: Proceedings, Hawk migration 4; 1983 March 24-27; Rochester, NY: 107-136.

Erdman, T.C.; Brinker, D.F. 1997. Increasing mist net captures of migrant Northern Saw-whet Owls (*Aegolius acadicus*) with an audiolure. In: Duncan, J.R.; Johnson, D.H.; Nicholls, T.H., eds. Biology and conservation of owls of the northern hemisphere: 2d international symposium; 1997 February 5-9; Winnipeg, Manitoba. Gen. Tech. Rep. NC-190. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station: 533-544.

Mueller, H.C.; Berger, D.D. 1967. Observations on migrating Saw-whet Owls. Bird Banding. 38(2): 120-25.

Robbins, S.D. 1991. Wisconsin birdlife. Madison, WI: University of Wisconsin Press. 736 p.

The Influence of Broadcast Tape-recorded Calls on Captures of Fall Migrant Northern Saw-whet Owls (*Aegolius acadicus*) and Long-eared Owls (*Asio otus*)

David L. Evans[1]

Abstract.—Nocturnal netting operations have been conducted at the Hawk Ridge Nature Reserve since 1972. From 1988 to 1992 a recording of human whistles simulating the calls of fall migrant Northern Saw-whet Owls (*Aegolius acadicus*) was broadcast on a random, on or off, half-night basis. Mist net captures of Saw-whet Owls increased about fourfold during the broadcast sessions, while captures of Long-eared Owls (*Asio otus*) decreased as much as 24 percent.

Broadcast tape-recorded calls (audiolure) have been widely utilized during the breeding season to attract and/or census territorial raptors. The employment of an audiolure to attract fall migrant Northern Saw-whet Owls (*Aegolius acadicus*) was initiated in 1986 at the Little Suamico Ornithological Station near Green Bay, Wisconsin, increasing capture rate by about a factor of 10 (T. Erdman, pers. comm.). To further investigate the effects of the audiolure, I broadcast a tape-recorded call on a random, on or off, half-night basis from 1988-1992.

METHODS

Trapping by mist net ('CTX', Association of Field Ornithologists) was conducted nightly from mid-September to mid-November at the Hawk Ridge Research Station, Hawk Ridge Nature Reserve, Duluth, Minnesota beginning in 1972. The study area, net placement, and owl capture techniques are described in Evans (1980). From 1988 to 1992 I broadcast a tape recording of human whistles simulating the calls of fall migrant Saw-whet Owls, as heard in previous years when large numbers of migrants were apparent (see below). The tape was played in a cassette car stereo powered by a 12 volt deep cycle marine battery and broadcast in the trapping area with a 4 x 8 inch (10.25 x 20.5 cm) speaker. On a random half-night basis (before or after midnight CST), netting was conducted either passively or with the audiolure being broadcast (on a random basis). Thus, the four treatment groups implemented were: evening with no broadcast (eve off), morning with no broadcast (morn off), evening with audiolure (eve on), and morning with audiolure (morn on).

RESULTS

A total of 3,708 Saw-whet Owls were captured during the 5-year period: 724 (19.5 percent) passively and 2,984 (80.5 percent) with the audiolure (table 1). Adjusting for an unequal number of treatment groups (100 eve off, 89 morn off, 97 eve on, 99 morn on) resulted in the following values for number of owls caught per half-night: 4.59/eve off, 2.97/morn off, 15.63/eve on, and 14.83/morn on. The proportion of owls caught during morning was 65 percent of evening while netting passively but increased substantially to 95 percent with the audiolure. We also noted a change in the juvenile to adult ratio when playing the audiolure. While netting passively the ratio was 0.83. For both groups, the ratio increased slightly from evening to morning, from 0.55 to 0.59 with the tape off, and from 0.79 to 0.87 with the audiolure. With the audiolure on, we caught 5.16 times as many juveniles and 3.53 times as many adults.

Initial concerns that the audiolure would result in increased numbers of recaptures, and possible interference with migration, proved unfounded. Numbers of recaptures during the same night were 37 for eve off, 56 for morn off, 78 for eve on, and 157 for morn on. The larger

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Table 1.—*Captures of Northern Saw-whet Owls* (Aegolius acadicus) *at Hawk Ridge, Minnesota, comparing passive and broadcast audiolure netting between evening (eve) and morning (morn).*

Year	Eve off	Morn off	Eve on	Morn on
1988	68	57	250	274
1989	63	56	595	388
1990	119	70	184	207
1991	80	49	363	358
1992	130	32	124	241
Total	460	264	1,516	1,468

numbers in the morning occur predominantly in the last hours before sunrise and appear to be owls that do not resume migration and may be searching for a place to roost. An additional 35 owls were recaptured one or more nights later: 16/eve off, 2/morn off, 14/eve on, and 3/morn on. The bulk of those recaptured in the evening (usually early evening) were those that had been released late the previous morning. Seven of the 35 owls were recaptured more than one day later; two at 3 days, two at 6 days, two at 9 days, and one at 10 days later. Expressed as a percentage of total owls caught per period, recapture rates were 11.6/eve off, 22.0/morn off, 6.1/eve on, and 10.9/morn on, thus, roughly half with the audiolure on.

Playing the audiolure appeared to have a detrimental effect on the capture of Long-eared Owls (*Asio otus*), with values per half-night at 0.84/eve off, 0.74/eve on, 0.88 morn off, and 0.67 morn on. Thus, with the audiolure on, we caught 12 percent fewer Long-eared Owls in the evening and 24 percent fewer in the morning.

DISCUSSION

Broadcasting the audiolure increased capture rates of fall migrant Saw-whet Owls about fourfold at Hawk Ridge, with juvenile owls more responsive to the tape than adults. It appears that the attraction to the audiolure is related to interactions of Saw-whet Owls when large concentrations occur. Prior to using the audiolure, we commonly heard saw-whets calling on nights when we had high capture rates. None of the three major owl banding stations in Wisconsin, which typically caught considerably fewer owls, had ever heard Saw-whets calling in the fall (T. Erdman, pers. comm.).

The considerable increase in owls caught in the morning when the audiolure was playing suggests that migration occurs at higher altitudes (above mist net level) later in the night, with hunting and feeding activities occurring at lower altitudes earlier in the night. The moderate increase in the proportion of juveniles caught in the morning may reflect their relative inexperience in hunting, thus resulting in them spending more time at lower altitudes searching for prey.

The decrease in Long-eared Owl captures, and why the decrease differs between evening and morning, is puzzling. Whether this suggests an actual avoidance of the audiolure or merely reflects the increased human activity involved in removing greater numbers of Saw-whet Owls is unknown.

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LITERATURE CITED

Evans, D.L. 1980. Multivariate analyses of weather and fall migration of Saw-whet Owls at Duluth, Minnesota. Fargo, ND: North Dakota State University. 49 p. M.S. thesis.

Monitoring Boreal Forest Owls in Ontario Using Tape Playback Surveys with Volunteers

Charles M. Francis and Michael S. W. Bradstreet[1]

Abstract.—Long Point Bird Observatory ran pilot surveys in 1995 and 1996 to monitor boreal forest owls in Ontario using roadside surveys with tape playback of calls. A minimum of 791 owls on 84 routes in 1995, and 392 owls on 88 routes in 1996; nine different species were detected. Playback improved the response rate for Barred (*Strix varia*), Boreal (*Aegolius funereus*), Northern Saw-whet (*Aegolius acadicus*) and possibly Great Gray (*Strix nebulosa*) Owls, and reduced variance among surveys for Barred Owls. Relatively few, long stops produced the most efficient survey for Barred Owls, while more numerous, shorter stops were optimal for Boreal and Northern Saw-whet Owls. Power estimates suggest that about 50 routes per species should be adequate to detect a uniform 20 percent decline over 10 years (2.2 percent per year) for Boreal and Northern Saw-whet Owls, and a 50 percent decline for Barred and Great Gray Owls (6.7 percent per year). However, some species were detected on many fewer than 50 routes, and models of uniform population changes may not be relevant for owls. For example, 60-80 percent fewer Northern Saw-whet and Boreal Owls ($P < 0.001$) were detected in 1996 than 1995 on routes that were run in both years, possibly related to emigration of many of these owls out of the study areas the preceding winter.

The Ontario Ministry of Natural Resources (OMNR) is responsible for the management of timber and natural resources, including wildlife, in much of central and northern Ontario. Under the terms of the Class Environmental Assessment of Timber Management on Crown Land in Ontario, the OMNR is required to monitor population trends of representative vertebrate species that are dependent upon forest habitats. There are several reasons why owls may be appropriate indicator species. First, some owls (such as the Spotted Owl, *Strix occidentalis*, in western North America) are known to be sensitive to logging and forest fragmentation. Second, some Ontario species are relatively rare. The Great Gray Owl (*Strix nebulosa*) was designated as Vulnerable in Canada until recently, while the Boreal Owl (*Aegolius funereus*) was considered too poorly known to be assigned a status in Ontario (Austen *et al.* 1994). Finally, as top predators, owls may also be sensitive to accumulations of toxins or other contaminants in the environment and thus may be useful as overall environmental indicators.

Most owl species, particularly species breeding in the boreal forests of Ontario, are not well monitored by other continental monitoring programs. Breeding Bird Surveys are conducted in the early morning and detect relatively few nocturnal species. Christmas Bird Counts detect some owls, but few such counts are conducted in northern Ontario, and the time spent "owling" on those counts is not standardized, so the results may be hard to interpret. Some owls, such as the Northern Saw-whet Owl (*Aegolius acadicus*), can potentially be monitored at migration monitoring stations, but the adequacy of those programs for monitoring this species has not been evaluated. Furthermore, because the breeding grounds of birds caught on migration are not known, it is difficult to tie population changes of migrants to specific land management practices.

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A review of various monitoring methods suggested that a roadside playback survey would likely be the most effective monitoring technique for boreal forest species of owls in Ontario (Shepherd 1992). Similar surveys have been carried out in Manitoba and adjacent Minnesota since 1991 (Duncan and Duncan 1991, 1993) and in the Red Lake district of Ontario since 1993 (Gilmore and MacDonald 1996). As a result, Long Point Bird Observatory was contracted by the OMNR to coordinate a pilot study in March-April of 1995 and 1996 to test the feasibility of a volunteer-based roadside survey to monitor owl populations in Ontario. In this paper we evaluate various aspects of the design of the survey and consider its power and adequacy for detecting population trends of Ontario owls.

METHODS

Survey Design

The basic survey design asked volunteers to select routes along plowed secondary roads through forested areas, and drive these routes starting one-half hour after sunset, stopping at regular intervals to survey owls. Volunteers were asked to choose a night with little wind (0-3 on the Beaufort Scale), with no precipitation, and when the temperature was not too cold (above -15˚C). Within the range of conditions surveyed, after correcting for date, we detected no correlations between weather conditions and numbers of owls reported, so we feel this component of the standardization was probably adequate.

At each stop, silent listening periods alternated with playback of selected target species of owls. Different survey protocols were established for northern Ontario (north of 47°N) and central Ontario, based on differences in the expected species in each region and their anticipated response rates. In both regions, calls of Boreal Owls were broadcast to elicit responses from Boreal Owls as well as from Northern Saw-whet Owls. The latter may respond to Boreal Owl calls, whereas the converse is believed not to be true (Shepherd 1992). In the northern region this was followed by a broadcast of Great Gray Owl calls. The Great Gray Owl was targeted because at the time it was designated as Vulnerable, and so that our surveys across northern Ontario could be compared to surveys already conducted in northwestern Ontario and southeastern Manitoba. Moreover, the Great Gray Owl call may elicit responses from Long-eared (*Asio otus*), Barred (*Strix varia*), or Great Horned (*Bubo virginianus*) Owls, in addition to Great Gray Owls. In the north, the playback protocol consisted of: 60 seconds silent listening to detect spontaneously calling owls, then 20 seconds of Boreal Owl call, then 60 seconds listening, then 20 seconds of Great Gray Owl, then a final 60 seconds of listening.

In the central region, where few Great Gray Owls were to be expected, the second species broadcast was the Barred Owl. Previous studies have indicated that Barred Owls may respond only very slowly to broadcasts (McGarigal and Fraser 1985), so the protocol was designed to include a very long listening period after the broadcast: 60 seconds listening, 20 seconds of Boreal Owl, 60 seconds listening, 20 seconds of Barred Owl, 120 seconds listening, 20 seconds of Barred Owl, and 480 seconds listening. The central region broadcast tape was modified in 1996 to test whether changes in two aspects of the playback protocols would improve response rates. One side of the tape used the same protocol as 1995, but with the final listening period divided into four intervals of 120 seconds each, separated by soft beeps. For the other side of the tape, Northern Saw-whet Owl calls were substituted for Boreal Owls, to test whether Northern Saw-whet Owls would respond better to conspecific broadcasts (because virtually no Boreal Owls had been detected in central Ontario in 1995 anyway). In addition, the number of broadcasts of Barred Owls was increased: the final 6 minutes was broken into three 120 second periods of 20 seconds of Barred Owl calls and then 100 seconds listening. Each protocol was usually played at alternate stops.

In northern Ontario, routes consisted of 25 stops spaced at 0.8 km intervals in 1995, but this was changed to 20 stops at 1.6 km intervals in 1996, to reduce the number of owls counted at more than one stop. Some routes in 1996 had slightly fewer stops because some of the available plowed roads could not accommodate the full length. In central Ontario, routes consisted of 10 stops at 2.0 km intervals in both years.

Surveyors were asked to survey each route twice, with the first survey window in early- to mid-March, and the second in early- to mid-April. In 1996, many routes in northern Ontario were surveyed again during a third window in late-April to early May. This survey was added in response to low numbers on the earlier surveys to determine whether owls might have been slow returning north because of the relatively cold, snowy winter, or because there had been an exceptional southwards movement the preceding winter (Ridout 1997).

Analysis Methods

Surveyors recorded the number of owls of each species detected during each time interval of the tape playback, as well as the total at each stop. In 1996, the form was designed to record the precise intervals when each individual owl was detected. In 1995, the information was slightly less complete and the time when a new owl started calling sometimes needed to be estimated.

To evaluate the effects of playback for Boreal, Northern Saw-whet and Great Gray Owls, we compared the total number of calls in the minute preceding any playback with the total number in the minute following playback of each species' call (or for Northern Saw-whet Owl, either its own or Boreal Owl calls). For Barred Owls, we used a similar procedure, but we used the combined total from the first 2 minutes (before and after Boreal/Saw-whet Owl playback) for comparison with the 2-minute interval after the first Barred Owl playback. For statistical testing, we excluded owls heard in both time periods (which would not be independent), and used a chi-square test to compare whether the number of owls calling only before playback was the same as the number calling only after playback. Because we had a one-tailed alternative hypothesis (that there would be more calling after playback), we created an approximate one-tailed test by halving the *P*-values if the difference was in the expected direction. To evaluate stop duration, we compared the proportions of owls that were first detected during each time interval.

To determine population changes, and estimate the power of the survey for detecting trends, two approaches were used. For comparing population indices between any 2 years, a combined ratio estimator was used, which consisted of the ratio of the total number of owls detected in each year on routes that were run in both years. The confidence limits and variance were estimated by boot-strapping, using routes as the sampling unit. A similar approach was used to compare numbers between survey windows within a year. For detecting long-term population trends, we assumed the data would be analyzed using log-linear route regression. This involves taking the log of all numbers (after adding a constant to avoid problems with log 0—we used 0.23 following Collins 1990), then using linear regression for data from each route, and finally calculating the mean slope across all routes. We used Monte Carlo simulations, as well as analytical techniques (John R. Sauer, pers. comm.) to estimate the relationships between variance after a 1-year interval (2 years of surveys) and variance after 5- or 10-year intervals, assuming a uniform, consistent population change across all routes and years. We then used the formulas in Snedecor and Cochrane (1967:113) to estimate the magnitude of change that could be detected based on these variance estimates with 80 percent power ($\beta = 0.8$) and a significance level of $\alpha = 0.05$. For analyzing annual changes, we used the maximum count for each species recorded in any of the survey windows for a particular year and route. This approach is not ideal, because not all routes were surveyed in all survey windows, but it did allow us to use as many routes as possible for power analyses.

The method of log-linear route regression has been shown to be flawed for various reasons, including sensitivity to the choice of constant added (Link and Sauer 1994). Link and Sauer (1994) proposed an alternative analysis technique using estimating equations, but this method requires enough data so that most routes have at least two non-zero years. We found we could not reliably use data from only two years of surveys to estimate the variance for longer periods with this method. Based on long-term data from the Breeding Bird Survey, precision of trend estimates derived from estimating equations tended to be slightly lower than that derived from log-linear route regression (Link and Sauer 1994), so the power of our surveys may be slightly less than we indicate here.

RESULTS

Effectiveness of Volunteer Surveys

The survey involved 73 volunteer surveyors in 1995 and 74 in 1996, usually accompanied by assistants. Many of the volunteers surveyed in both years, and indicated an interest in continuing with the survey into the future. In 1995, 84 routes were surveyed, 78 percent of them in both of the first two survey windows, while in 1996, 88 routes were surveyed, 76 percent of which were covered in both of the first two survey windows. However, only 44 routes were covered in both years. This high turnover in routes was due partly to replacement of routes that proved to be unsuitable in 1995, so we can hope for a lower turnover as the survey becomes more firmly established.

Owls were detected on most routes, with a total of at least 791 individuals of eight species in 1995 and 392 individuals of nine species in 1996. The most commonly encountered owls were Northern Saw-whet, Boreal and Barred Owls, though moderate numbers of Great Gray and Great Horned Owls were also detected (table 1). Only 5 routes in 1995 and 12 routes in 1996 failed to find owls on any survey (although on some of the others no owls were detected during one or more survey windows).

Table 1.—*Minimum number of different owls detected on the Ontario nocturnal owl survey along 84 routes in 1995 and 88 routes in 1996. The numbers given are the sums of the highest count for each species on each route during any of the survey windows in each year. The actual number of owls detected was probably higher, because owls detected during one survey window on a route were not necessarily the same birds as were detected on later survey windows. Note that these numbers are not reliable for estimating trends, because only 44 of these routes were surveyed in both years, and routes were not randomly selected.*

	Minimum number detected each year	
Owl species	**1995**	**1996**
Northern Saw-whet Owl	321	97
Boreal Owl	202	62
Great Gray Owl	28	15
Barred Owl	149	153
Great Horned Owl	74	39
Long-eared Owl	8	19
Short-eared Owl	7	2
Northern Hawk Owl	0	3
Eastern Screech-owl	2	2

Survey Design

Effects of Playback

For Boreal, Northern Saw-whet and Barred Owls, significantly more birds were detected after playback than before playback in both years (table 2). For Great Gray Owls, there was no evidence of any effect of playback in 1995, but in 1996 playback did seem to increase response, although the sample size was small. Additional data from Doug Gilmore (pers. comm.), who used a similar protocol to survey owls around the Red Lake district in northern Ontario in 1993 and 1994, indicated a substantial increase from before to after playback in the number of Great Gray Owls detected, from 5 to 13 in 1993, and from 26 to 46 in 1994.

For Boreal and Northern Saw-whet Owls, the estimated proportion of additional owls detected as a result of playback was only 16-19 percent, reflecting the large number of spontaneously calling owls. However, for Barred Owls, playback led to an increase of 50 percent in the number of owls detected during the first 2 minutes after playback. In addition, many owls that were detected in later listening intervals may also have been stimulated by playback, although the magnitude of the effect cannot be measured except by comparison with surveys not using playback.

With the 1996 data, we attempted to test whether Northern Saw-whet Owls would respond better to their own call or to that of Boreal Owls, in the Central Ontario region. However, during 1996 in that region we had so few Northern Saw-whet Owls that we could not even demonstrate an effect of playback of either species. Considering only the minute before and after playback, the numbers detected during the 1 minute before and after playback of each species were almost identical: 18 before and 17 after the Boreal Owl playback, and 17 before and 17 after the Northern Saw-whet Owl playback. If we consider the total numbers of owls first detected before and after playback (including the several minute listening period for Barred Owls), the numbers become 18 versus 16 and 17 versus 21,

Table 2.—*Numbers of responses of owls during the listening interval before and after playback of their own calls for Boreal, Great Gray and Barred Owls, and either their own or Boreal Owl calls for Northern Saw-whet Owls on the Ontario Nocturnal Owl Survey, 1995-1996.*

		Total owls detected in each interval		**Number detected only in one interval**		
Species	**Year**	**Before**	**After**	**Before**	**After**	**P**[1]
Boreal Owl	1995	206	234	49	77	0.006
	1996	52	66	11	25	0.01
Northern Saw-whet Owl	1995	262	305	61	104	0.004
	1996	56	73	9	26	0.002
Barred Owl	1995	43	60	17	34	0.009
	1996	49	77	10	38	0.001
Great Gray Owl	1995	19	19	9	9	n.s.
	1996	5	11	2	8	0.03

[1] Probability (one-tailed chi-square test) that the number detected only before playback was the same or higher than the number detected after playback, relative to the alternative hypothesis that more owls called after playback.

respectively, but while this is in the direction of a stronger effect of Saw-whet Owl playback, it is not significant.

We also tested whether additional playback increased response rates of slow responding Barred Owls. The numbers of Barred Owls detected before and after the third Barred Owl call (when the tapes began to differ) was 55 and 26 for the side with no additional calls, and 52 and 32 for the side with additional calls. While this is in the direction of suggesting better response rates with additional playback, it is not significant.

Stop Duration

All else being equal, the survey should be designed so that each surveyor will detect the maximum number of independent owls during a survey of a reasonable duration (3-4 hours). This involves selecting the optimal combination of waiting time at each stop, spacing between stops, and number of stops. For owls that respond quickly, more shorter stops may be preferred, while for slow responding owls, fewer longer stops may be preferred. For longer stops, the number of owls detected late in the listening period must be sufficiently high to justify the concomitant reduction in number of stops.

For Boreal Owls in northern Ontario, 65 percent of birds in 1995, and 56 percent in 1996 were first detected in the first minute before playback, and only 11 percent and 17 percent were first detected in the third minute (the final listening period). This suggests that prolonging stops would be unlikely to produce enough additional owls to justify any reduction in the number of stops. The results from Northern Saw-whet Owls from northern Ontario are similar, with 65 percent in 1995 and 48 percent in 1996 detected in the first minute, and only 11 percent and 12 percent first detected in the third minute. The data from central Ontario provided confirmation that a prolonged final listening period is not efficient for this species. In both years, listening for the final 8 minutes only increased the number of owls detected by about 30 percent over the number in the first 4 minutes. In contrast, listening for only 4 minutes and doubling the number of stops (which after allowing for travel time could be done in the same or less total survey time), would be expected to double the number detected (a 100 percent increase).

Response speed of Great Gray Owls could not be tested, because the listening period only extended for 1 minute after playback. However, for Barred Owls, a prolonged listening and playback period did appear to be worthwhile, based on data from central Ontario. In 1995, 80 owls were first detected in the final 8 minutes, as opposed to only 77 in the first 4 minutes. In 1996, the numbers were 91 in the final 8 minutes and 87 in the first 4 minutes. Breakdown of the last 8 minutes from 1996 indicates that 19 of these owls were not detected until the final 2 minutes. Based on these figures, the total number of Barred Owls detected would have been expected to have been fairly similar if there were twice as many stops of only 4 minutes duration. However, comparison of results from the first and second survey windows indicates that the prolonged listening period may reduce variation due to seasonal changes in calling propensity. In the first survey window in 1995, 45 owls were first detected in the first 4 minutes, and 28 in the final 8 minutes, while in the second survey window the proportions were strongly reversed: 32 and 52 respectively. The relative difference in the totals (73 versus 84) was less than the difference between the numbers detected only in the first 4 minutes (45 and 32). In 1996, the number of responses during the first 4-minutes and final 8-minutes was much more similar between survey windows (38 and 41 for the first window and 49 and 50 for the second window).

Stop Spacing

Increasing the stop spacing from 0.8 km to 1.6 km in northern Ontario led to fewer owls being detected at multiple stops. This decrease was most dramatic for Boreal Owls (57 out of 318 records of owls in 1995 were believed to have been birds that were detected at previous stops, compared with only 1 out of 97 in 1996) and for Northern Saw-whet Owls (30 out of 260 in 1995 compared with 0 out of 121 in 1996). For Great Gray Owls, 7 out of 33 records were believed to be duplicates in 1995, compared with 0 out of 16 in 1996. However, for Barred Owls there was no change in the number being heard from multiple stops (4 out of 40 in 1995 compared with 6 out of 39 in 1996). Apart from reducing the amount of duplication in the area being surveyed at each stop, increasing the spacing may also help to reduce variance associated with differences in judgment among observers as to which owls are duplicates. However, this came at the cost of reducing the number of stops (to 20 from 25), and some routes were unable to accommodate the overall increased length (due to insufficient plowed roads) and were run with fewer than 20 stops.

Survey Timing

The seasonal peak in calling appeared to differ between 1995 and 1996 for some owl species (table 3). For Boreal and Northern Saw-whet Owls, peak numbers were detected in the first window in 1995, but during the second or third survey window in 1996. For Barred Owls, the peak was higher on the later surveys in both years, while for Great Gray Owls no strong seasonal effects were evident, although the sample size was small.

To test the significance of these changes between any two survey windows, we restricted analysis to routes sampled during both

Table 3.—*Mean number of target species of owls per route for the first (early to mid-March), second (early to mid-April) and third (late April to early May) survey windows in central and northern Ontario, 1995-1996.*

		Survey window				
		1995		1996[1]		
Species	Region	1	2	1	2	3
Boreal Owl	North	4.34	1.98	0.46	0.9	1.79
Northern Saw-whet Owl	North	2.76	2.79	0.4	0.3	0.75
	Central	3.55	3.09	0.77	1.24	-
Barred Owl	North	0.44	0.43	0.23	0.33	0.5
	Central	2.18	2.47	1.87	2.61	-
Great Gray Owl	North	0.34	0.29	0.06	0.2	0.17
	Central	0.06	0.06	0.03	0.03	-
Number of routes	North	41	42	35	40	24
	Central	33	39	39	38	-

[1] The third survey window was added in 1996 for northern Ontario only, to determine whether owls that had moved southwards might have returned later in the season to breed.

windows. In 1995, the number of Boreal Owls detected declined by about half between the first and second window ($P < 0.01$ based on boot-strapped confidence limits from a combined ratio estimator). In 1996, an increase of a similar magnitude from the first to the second window in 1996 was not significant, but there was a highly significant ninefold increase (from 2 to 18 owls) between the second and third window on the 19 routes surveyed during both those windows ($P < 0.01$). For these same routes in 1996, there appeared to be a substantial decline in Great Gray Owls from the second to the third window from 6 to only 1 ($P < 0.01$). However, a similar decline was not apparent if all routes were considered (table 3) suggesting this result must be treated cautiously, and may be a small sample artifact. None of the seasonal changes in other species were significant based on this test.

Population Changes and Survey Power

Based on the highest count recorded during any survey window for routes run in both years, the numbers of Northern Saw-whet Owls detected in 1996 were only 19 percent of those in 1995 for northern Ontario, and 41 percent of those in 1995 for central Ontario ($P < 0.001$ based on boot-strapped confidence limits from a combined ratio estimator). Boreal Owl counts in northern Ontario in 1996 were 27 percent of their level in 1995 ($P < 0.001$). Note that these ratios do not exactly match counts in table 1, because many routes were not run in both years. Numbers of owls of other species detected did not differ significantly between years.

Using variance estimates derived from these between-year changes, we estimated the percentage population change that the survey could detect over a 10-year interval, assuming a uniform population change across the range (table 4). With 50 routes per region, the survey should be able to detect a population change of 20 percent or less for Boreal and Northern Saw-whet Owls (representing a 1-2 percent change per year), while for Barred and Great Gray Owls the survey should be able to detect a 40-50 percent change. However, these sample sizes assume that routes are run in every year, and only include routes for which the species was recorded at least once (i.e., constant zero routes do not contribute to the analysis). For Great Gray Owls, the actual number of relevant routes for the first 2 years was only 8. Furthermore, the power may be less if populations are not changing uniformly across the range (i.e., increasing on some routes and decreasing on others). These estimates are also very sensitive to the variance estimates, which are not very precise based upon only two years of data.

Table 4.—*Estimated percentage population change that the Ontario survey could be expected to detect with an 80 percent probability at $P < 0.05$ over a 10-year period (11 years of surveys)[1]. Power was estimated by extrapolating from the observed variance between 1995 and 1996 in the maximum numbers of owls detected for routes run in both years, assuming log-linear route regression analyses. Note that these estimates should be considered only as very general guidelines, because they are very sensitive to the variance estimates (which are not very precise), and they assume a uniform decline over time and across the range. Note also that the number of routes only includes routes on which a species is detected in at least some years.*

		Number of routes		
Species	**Region**	**25**	**50**	**100**
Boreal Owl	North	17	12	8
Northern Saw-whet Owl	Central	26	18	12
Northern Saw-whet Owl	North	8	5	4
Great Gray Owl	North	69	48	34
Barred Owl	Central	46	32	22
Barred Owl	North	63	44	31

[1] Numbers given represent the cumulative change in the population. In annual terms, a 20 percent total decline over 10 years represents about 2.3 percent per year, while a 50 percent total decline represents about 6.7 percent per year.

DISCUSSION

This survey was relatively popular with volunteers and produced a large amount of data on nocturnal owls much more economically than could have been achieved using paid surveyors. Furthermore, power analyses suggest that moderate long-term population trends should be detectable with reasonable power for at least some target species (see table 4). Use of playback was effective in increasing response rates, thus potentially improving the efficiency of the survey. Play-back combined with a prolonged listening period may also reduce variance due to seasonal changes in calling propensity of Barred Owls.

However, the survey does have a number of drawbacks, both biological and logistical. Perhaps the most substantial limitation is that for some species, such as Boreal and Northern Saw-whet Owls, changes in the numbers of owls detected may be hard to interpret. The dramatic decline in the number of these owls detected in 1996 compared to 1995 may have been related to southward emigration of many birds the preceding winter. Reports from bird-watchers in southern Ontario indicate a very large "invasion" of Great Gray Owls, as well as moderate numbers of Boreal Owls and Hawk Owls (Ridout 1997). This was presumably related to a decline in prey numbers (microtine rodents) combined with exceptional snow fall. Low numbers of birds during the surveys, even for species such as Northern Saw-whet Owls that are probably largely migratory most years anyway, may have been related to failure of the birds to return (perhaps due to deep snow or to continued low numbers of prey), or to high mortality over the winter. The tendency for Boreal Owls to be detected more frequently in the last survey window in 1996 suggests a late return of some individuals.

Similar annual variation in numbers calling has been found in previous studies of owls, and has been postulated to be linked to small mammal cycles (Palmer 1987). Fluctuations in prey supply have been shown to affect both breeding and survival rates for at least some species of owls including Great Horned Owls in Saskatchewan (Houston and Francis 1995) and Boreal Owls in Europe (Korpimäki 1985, Sonerud *et al.* 1988). Additional data would be required to determine the extent to which the apparent population changes observed on this survey were due to overwinter mortality (i.e., a real population decline), late return or non-return of owls that had emigrated (but which were still alive and could return in later years), or low calling frequency of birds that were present in the study area, perhaps because they were not breeding. Regardless of the explanation, fluctuations in counts affect the power of this survey (or any other type of survey) to detect long-term population trends. Many years of data would be required to differentiate short-term cycles from long-term declines, regardless of the number of routes and precision of the survey.

There were also a number of logistical limitations to the surveys. Ideally, route selection should be randomized to ensure that trends along selected routes are representative of population trends throughout the region. However, for several reasons it was necessary to ask volunteers to select their own routes. Relatively few suitable roads were available in the region, especially in the north. The suitability and condition of these roads in winter was generally known to the local people, but not to the survey organizers. Furthermore, the pool and distribution of qualified volunteers was somewhat limited. For a nocturnal winter survey there are limits to how far one can expect volunteers to travel to carry out a survey. This necessarily results in a higher density of routes within 1-2 hours drive of population centers.

Because most volunteers selected routes on the basis of generally suitable habitat, rather than specific known locations of owls, there is no particular reason to believe trends on selected roads will differ from those on random roads. In any case, with any roadside survey (including well randomized ones such as the Breeding Bird Survey) it is necessary to assume that trends along roadsides are the same as those away from roadsides—probably a greater limitation than any bias caused by non-random route selection in this case.

In addition to route selection, route continuity is a potential problem. Many of the available roads are logging roads, which are only kept plowed in winter if they are in use. Because of changes in locations of logging, some routes surveyed in 1995 were not available in 1996. Also, there may be problems finding replacement surveyors for particular routes if any of the surveyors move out of the area, owing to relatively low human population densities in some areas.

Use of playback was effective in increasing the response rate and, at least for Barred Owls, appeared to help reduce variance due to seasonal changes in calling propensity. However, it does carry the cost of potentially introducing long-term bias due to changes in playback units and/or tapes. Improvement of a broadcast tape used for a similar roadside survey of Red-shouldered Hawks (*Buteo lineatus*) was associated with a 100 percent increase in the number of hawks detected between 1994 and 1995 (Heagy and Francis 1995). For the owl survey, because volunteers were asked to supply their own broadcast units, changes in these units over time could also lead to bias, especially given the general trend for electronic goods to get cheaper and more powerful over time.

For several species that had relatively high spontaneous calling rates (including Boreal, Northern Saw-whet, Great Gray, and Great Horned Owl) a calling survey without playback would probably be only slightly less efficient, and may be preferable because of the reduced need for equipment and the reduced risk of introducing long-term bias. For Barred Owls, a high proportion of birds were detected late in the listening period, suggesting playback may substantially increase detections, and playback also appeared to reduce seasonal variation. However, surveys incorporating longer passive listening periods would be required to estimate the relative efficiency of a survey without playback. It also needs to be determined whether volunteers would prefer, and hence be more likely to participate in, an active survey involving playback, with at least a slightly higher response rate, compared to a survey based entirely on passive listening.

Despite various limitations, we believe this survey provides valuable information in a cost-effective way on Ontario owl populations. Based on data gathered in the first 2 years, the general survey design, in terms of numbers, duration, and spacing of stops, appears to be adequate—it was quite sufficient to detect some major fluctuations in numbers of the two smaller species. Numbers of routes should be increased if possible to detect trends of some of the rarer species such as the Great Gray Owl, and to allow for attrition of routes over time. This will involve continuing to encourage as many participants as possible in the survey. It would potentially be more efficient to reduce the survey to one survey window per year, but based on annual variation in the seasonal calling peaks observed during the first 2 years, it may not be possible to select a single optimal time period for the survey each year. As such, we plan to continue with two surveys per year in the near future, to learn more about annual variation in calling phenology.

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LITERATURE CITED

Austen, M.J.W.; Cadman, M.D.; James, R.D. 1994. Ontario birds at risk: status and conservation needs. Don Mills, ON: Federation of Ontario Naturalists and Long Point Bird Observatory. 165 p.

Collins, B.T. 1990. Using re-randomizing tests in route-regression analysis of avian population trends. Biol. Rep. 90: 63-70. Washington, DC: U.S. Fish and Wildlife Service.

Duncan, P.A.; Duncan, J.R. 1991. Nocturnal audio/playback owl survey of southeastern Manitoba and adjacent Minnesota: 1991 progress report. Winnipeg, MB: Manitoba Department of Natural Resources. 8 p.

Duncan, P.A.; Duncan, J.R. 1993. Manitoba's nocturnal owl survey: 1993 progress report. Winnipeg, MB: Manitoba Department of Natural Resources. 8 p.

Gilmore, D.; MacDonald, C. 1996. Northern forest owl survey: Red Lake. Ontario Birds. 14: 91-99.

Heagy, A.; Francis, C.M. 1995. Red-shouldered Hawk and spring woodpecker survey—1995 progress report to Ontario Ministry of Natural Resources. Port Rowan, ON: Long Point Bird Observatory. 47 p.

Houston, C.S.; Francis, C.M. 1995. Survival of Great Horned Owls in relation to the snowshoe hare cycle. Auk. 112: 44-59.

Korpimäki, E. 1985. Rapid tracking of microtine populations by their avian predators: possible evidence for stabilizing selection. Oikos. 45: 281-284.

Link, W.A.; Sauer, J.R. 1994. Estimating equations estimates of trends. Bird Populations. 2: 23-32.

McGarigal, K.; Fraser, J.D. 1985. Barred Owl responses to recorded vocalizations. Condor. 87: 552-553.

Palmer, D.A. 1987. Annual, seasonal, and nightly variation in calling activity of Boreal and Northern Saw-whet Owls. In: Nero, R.W.; Clark, R.J.; Knapton, R.W.; Hamre, R.H., eds. Biology and conservation of northern forest owls: symposium proceedings; 1987 February 3-7; Winnipeg, Manitoba. Gen. Tech. Rep. RM-142. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 162-168.

Ridout, R. 1997. Ontario regional report winter 1995/1996. National Audubon Society Field Notes. 51: in press.

Shepherd, D. 1992. Monitoring Ontario's owl populations: a recommendation—report to Ontario Ministry of Natural Resources. Port Rowan, ON: Long Point Bird Observatory. 82 p.

Snedecor, G.W.; Cochran, W.G. 1967. Statistical methods. 6th ed. Ames, IA: Iowa State University Press.

Sonerud, G.A.; Solheim, R.; Prestrud, K. 1988. Dispersal of Tengmalm's Owl *Aegolius funereus* in relation to prey availability and nesting success. Ornis Scandanavica. 19: 175-181.

Great Horned Owl (*Bubo virginianus*) Productivity and Home Range Characteristics in a Shortgrass Prairie

Rosemary A. Frank and R. Scott Lutz[1]

Abstract.—We studied movements and breeding success of resident Great Horned Owls (*Bubo virginianus*) at the Rocky Mountain Arsenal National Wildlife Refuge from 1994-1996. We captured adult owls prior to nest initiation and outfitted them with radio transmitters. Twelve, 5, and 11 pairs nested each year, respectively. Eleven nests successfully hatched and produced 24 owlets in 1994, 3 nests produced 6 owlets in 1995, and 10 nests produced 29 owlets in 1996. We documented three cases in which a single parent successfully fledged owlets. We recorded three cases of nest site reuse. Ninety-five percent adaptive kernel mean home range size did not differ between ages or sexes.

We studied movements and breeding success of resident Great Horned Owls (*Bubo virginianus*) at the Rocky Mountain Arsenal National Wildlife Refuge from 1994-1996. The Rocky Mountain Arsenal is a large, open space in the midst of the Denver metropolitan area. The site was used for weapons production during World War II, and for pesticide production following the war. Production practices of that era led to soil and ground water contamination on the surrounding landscape. The site is being cleaned and transformed into an urban wildlife refuge through cooperative efforts by the United States Army, Shell Oil Corporation, and the U.S. Fish and Wildlife Service. The Great Horned Owl may be used by the U.S. Fish and Wildlife in their long term biomonitoring program on the Refuge. We collected productivity and home range information as part of a study to gather baseline data about Great Horned Owls on the Refuge.

STUDY AREA

The Rocky Mountain Arsenal National Wildlife Refuge (Refuge) is located in south-central Adams County, Colorado, and is bordered to the north and east by agricultural and commercial districts. Its southern border is adjacent to Denver city limits and is approximately 16 km northeast of the metropolitan area. The facilities encompass 6,900 ha of open grassland, rolling hills, and wetlands, providing an island of wildlife habitat in a heavily urbanized area. The Refuge supports diverse plant and animal communities and was designated to be an urban wildlife refuge in 1992.

The climate is semi-arid, with low humidity, light rainfall, and moderate to high winds. Average annual precipitation is approximately 38 cm. Elevation on the Refuge ranges from 1,534 m to 1,625 m above sea level. Historically, the area was covered by short grass prairie vegetation. The vegetation on the Refuge is currently dominated by five major communities: cheatgrass (*Bromus* spp.)/perennial grassland, weedy forbs, cheatgrass /weedy forbs, crested wheatgrass (*Agropyron cristatum*), and native perennial grassland (Environmental Science and Engineering 1989).

TRAPPING AND BODY SIZE

We trapped adult Great Horned Owls from February through late April in 1994, late December through late March in 1995, and early January through April in 1996. We used quonset-shaped bal-chatri traps (Berger and Hamerstrom 1962) with avian and rodent lures, pigeon harnesses, leghold traps, and dho gaza traps (Bloom 1987) to trap adult owls. We captured 20 adult Great Horned Owls between 1994-1996. Seven of the owls were captured using bal-chatri traps with rodent and avian lures. We trapped six owls using pigeons in a harnesses with nylon nooses. During the incubation stage, we trapped three adult male owls using a dho gaza trap with a stuffed Great Horned Owl and a tape recording of Great Horned Owl calls as a lure. During the nestling stage, we captured two adult females and one adult male using a dho gaza trap and a live Red-tailed Hawk (*Buteo jamaicensis*) as the lure. We trapped one adult owl using a padded leghold trap with a rodent lure. Great Horned Owls, like most raptors, exhibit reversed sexual size dimorphism; the males are smaller than the females. As expected, adult females (1,388 g) were slightly larger than adult male owls (1,194 g) on the Refuge (table 1).

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PRODUCTIVITY

Nesting Success

Five to 12 nesting pairs have been documented on the Refuge per year (1990-1996) (USFWS 1994, Frank and Lutz 1997). In 1994, 1995, and 1996, 12, 5, and 11 pairs nested each year, respectively (table 2). In 1994, 12 pairs of Great Horned Owls initiated nests; three other pairs separated prior to the breeding season or failed to initiate nests. Of the 12 nesting pairs, one member from each of four pairs died prior to the next breeding season. One owl was electrocuted, but the causes of death were undetermined for the other three owls. In 1995, 11 pairs of owls exhibited signs of courtship and pair bonding, yet only five pairs initiated nests. It is uncertain whether this difference in breeding effort was a result of differences in environmental conditions between years, or due to the high number of newly established pairs. In 1996, 11 of 12 owl pairs on the Refuge initiated nests. Eleven nests hatched and produced 24 owlets in 1994, three nests produced six owlets in 1995 and 10 nests produced 29 owlets in 1996.

Nest Failures

We monitored four nest failures during the 3 years. All failures occurred during the

Table 1.—*Body measurements of adult Great Horned Owls captured at the Rocky Mountain Arsenal National Wildlife Refuge, near Denver, CO, 1994-1996.*

Measurement	Male (n=10)	Female (n=8)	P
Weight (g)	1,194.7 (27.7)[1]	1.388.3 (52.6)[2]	0.003
Wing chord (mm)	351.3 (5.6)	360.4 (9.2)	0.383
Tarsal width (mm)	10.1 (0.2)	10.6 (0.3)	0.211
Hallux length (mm)	22.3 (0.3)	23.8 (0.4)	0.010
Tail length (mm)	214.5 (4.6)	230.3 (7.6)	0.082
Culmen length (mm)	27.9 (0.6)	28.9 (0.5)	0.173

[1] Mean and (standard error)

[2] (n = 6)

Table 2.—*Number of pairs and reproductive parameters for Great Horned Owls on the Rocky Mountain Arsenal National Wildlife Refuge near Denver, CO, 1994-1996.*

	Year		
Parameter	1994	1995	1996
Pairs on Refuge	15	11	12
Pairs nesting	12	5	11
% Hatched	0.92	0.60	0.91
% Successful	0.92	0.60	0.91
Total young produced	24	6	29

incubation stage. In all cases, the adults survived and remained near the nest site after the failure. The first documented failure occurred in 1994. Two nests failed in 1995 and one nest failed in 1996. In three cases, we found small egg shell fragments in the nest structure. However, we were unable to determine if the eggs were depredated, or scavenged after being abandoned. We did not document any loss of chicks during the nestling period when chicks were observable (4-9 weeks).

Single Parent Nests

We documented three cases in which individual owls successfully fledged young. In 1995, an adult male from a nest in section 12 disappeared (fate unknown) early in the nestling stage. The female fed the two chicks; both fledged and dispersed off the Refuge. In 1996, a radio-marked male at a nest in the former South Plants production area of the Refuge died from dieldrin poisoning early in the nestling stage. The female fledged three chicks. However, all three were electrocuted within weeks of fledging. Also in 1996, an unradio-marked adult female died late in the nestling period from dieldrin poisoning. The male fledged three owlets. One chick later died after suffering a wing injury.

MOVEMENT

Site Fidelity

Twenty-eight Great Horned Owl pairs nested on the Refuge during 1994-1996 (fig. 1). Four nesting areas were used in two or more years. In three cases, the same nest structure was used in multiple years. In general, old raptor and Black-billed Magpie (*Pica pica*) nests were used as nesting structures. However, an artificial raptor nest structure was used in 1995 and 1996. Two pairs of owls nested in buildings in 1996. Two pairs of owls nested in crooks of large cottonwood trees with no nesting materials.

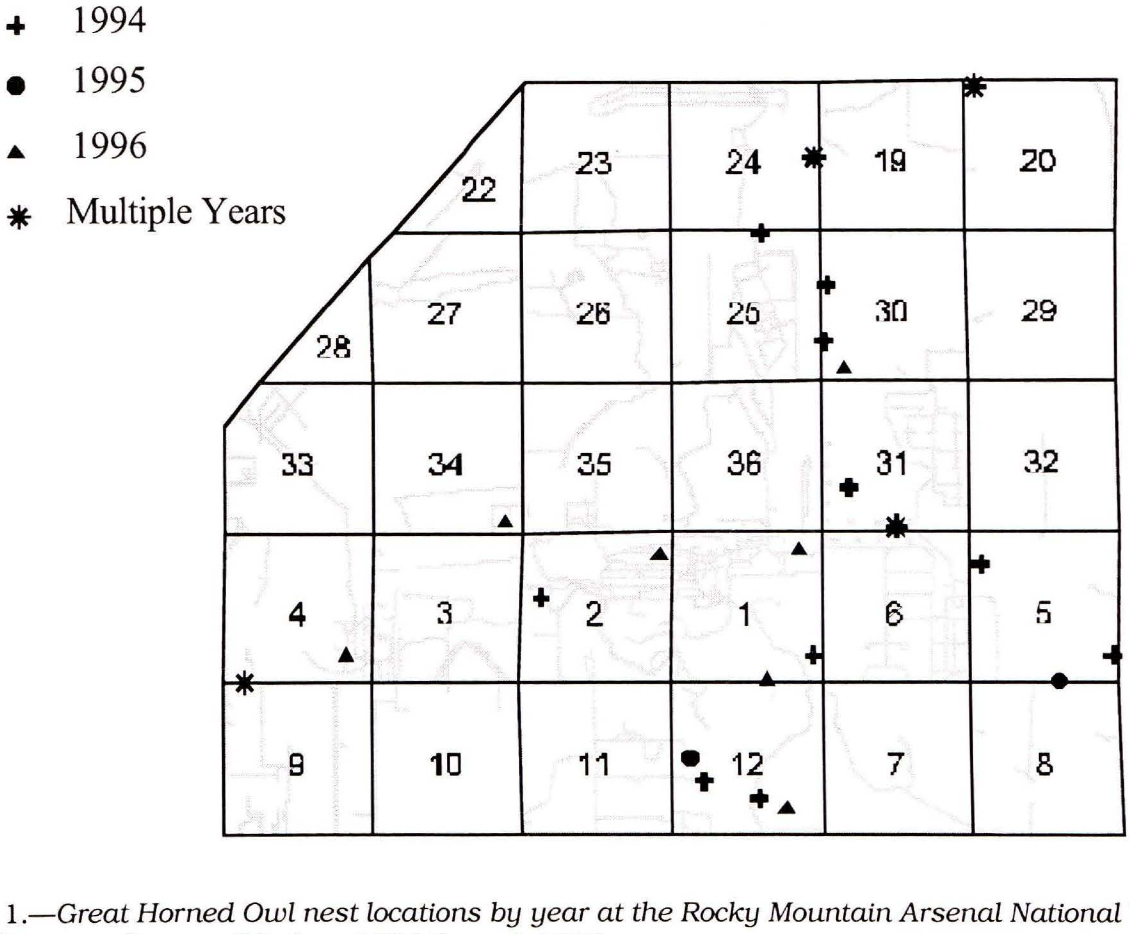

Figure 1.—*Great Horned Owl nest locations by year at the Rocky Mountain Arsenal National Wildlife Refuge near Denver, CO, from 1994 through 1996.*

Home Range Estimates

We collected 319 locations on nine adult and subadult owls in 1995 and 502 locations on 10 owls in 1996. We were able to calculate adaptive kernel home range (Worton 1989) estimates for seven owls in 1995 and nine owls in 1996. Home range estimates did not differ between years (50 percent home range contour, 67.43 ha [1995] vs. 61.00 ha [1996], t = 0.182, P = 0.858; 80 percent, 245.29 ha [1995] vs. 221.34 ha [1996], t = 0.219, P = 0.830; 95 percent, 671.86 ha [1995] vs. 612.67 ha [1996], t = 0.191, P = 0.852, 14 df) so we pooled them for analysis. The 50 percent home range contour estimate was greater for adult owls than subadult owls (75.97 ha vs. 27.25 ha, t= 2.186 P= 0.049, 14 df, fig. 2). We did not find any differences between sexes (fig. 2). Because of small sample sizes and fairly high variability, the power of these statistical tests was low (range = 0.07 to 0.21).

CONCLUSIONS

While the number of Great Horned Owl pairs on the Refuge remained somewhat constant over the 3 years of our study, we did observe some variation in the number of pairs that nested. We hypothesize that these variations might be due to differences in environmental conditions among years, or due to turnover within pairs. Owls tended to rely on existing stick structures for nest sites, but showed some adaptability by nesting in buildings and artificial structures. In three of 28 cases, the same nest structure was used in multiple years. All of the nest failures we observed occurred during the incubation stage. Even when one member of a pair died during the nestling period, a single parent (male or female) was able to successfully feed and protect nestlings until they fledged. Individual owl home ranges were variable in size. We could not distinguish any differences in home range size by age or sex.

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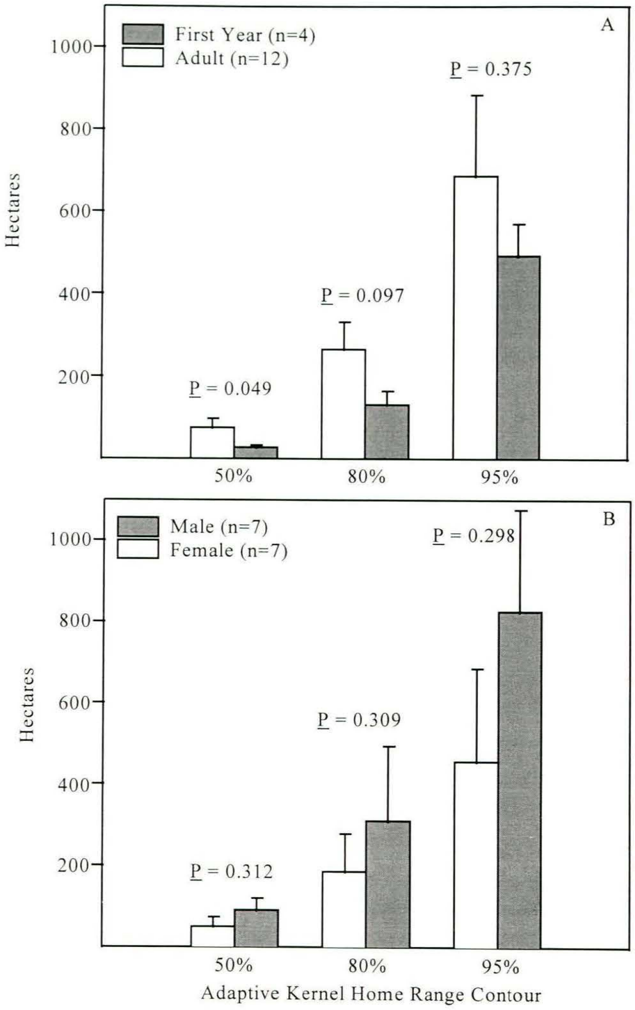

Figure 2.—*Adaptive kernel contour home range size estimates of Great Horned Owls by age (A) and sex (B) at the Rocky Mountain Arsenal National Wildlife Refuge near Denver, CO, in 1995 and 1996.*

LITERATURE CITED

Berger, D.D.; Hammerstrom, F. 1962. Protecting a trapping station from raptor predation. Journal of Wildlife Management. 36: 153-156.

Bloom, P. 1987. Capture and handling raptors. In: Pendleton, B.A.; Millsap, B.A.; Cline, K.W.; Bird, D.M., eds. Raptor management techniques manual. Natl. Wildl. Fed. Scientific and Tech. Ser. 10: 99-123.

Environmental Science and Engineering. 1989. Environmental Setting, section 2.0. Rocky Mountain Arsenal biota remedial investigation-draft final report, version 2.2.

Frank, R.A.; Lutz, R.S. 1997. Effects of environmental contaminants on Great Horned Owls at the Rocky Mountain Arsenal National Wildlife Refuge. Final Report submitted to United States Army and U.S. Fish and Wildlife Service, Rocky Mountain Arsenal National Wildlife Refuge. January 1997.

USFWS. 1994. U.S. Fish and Wildlife Service Rocky Mountain Arsenal Field Office Amendment 11 to the 1993 Fish and Wildlife Management Plan. July 1993.

Worton, B.J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology. 70: 164-168.

Size, Dimorphism, and Related Characteristics of *Ciccaba* Owls From Guatemala

Richard P. Gerhardt and Dawn McAnnis Gerhardt[1]

Abstract.—Tropical owls, being poorly studied, have been excluded from discussions of reversed size dimorphism. As part of a breeding and food habits study, we weighed and measured 20 Mottled Owls (*Ciccaba virgata*) and a mated pair of Black-and-white Owls (*C. nigrolineata*) in northern Guatemala. Mottled Owls exhibited pronounced dimorphism with respect to body mass, wing chord, and tail length. A mated pair of Black-and-white Owls was also quite dimorphic with respect to body mass. Mate choice in six pairs of Mottled Owls was not correlated with size (mass or wing chord). Since both species are highly insectivorous, they do not fit an alleged trend among owls toward increasing dimorphism with increased reliance on vertebrate prey. Indeed, our results are at odds with important assumptions or predictions of numerous hypotheses regarding the evolution of reversed size dimorphism in owls.

Whereas in most bird species, males are larger than females, in owls (Strigiformes) and other raptors (Falconiformes) females are generally the larger sex. More than 20 hypotheses have been advanced to explain the evolution of this reversed size dimorphism, or RSD (for a summary, see Andersson and Norberg 1981, Mueller and Meyer 1985, and Mueller 1986). To date, owl data used for advancing and testing these hypotheses and associated assumptions and predictions have come from studies of those species living in northern temperate zones. Such studies have almost exclusively dealt with 18 North American owl species and 13 owl species that breed in Europe (a total of 24 species, since 7 are found on both continents). This temperate bias is natural enough, since little information on owls outside these areas is available. None-the-less, this bias may have important implications on the validity and generality of the resulting hypotheses.

Most researchers and theorists agree that the most valid field measurement for discussions of dimorphism is body mass (Amadon 1977, Cade 1960, Earhart and Johnson 1970, McGillivray 1987, Mueller 1986), and McGillivray (1987) suggested that these be taken during the breeding season, since most hypotheses link the role of RSD to this critical period of the annual life cycle. Other measurements that have been analyzed for degree of dimorphism include wing length, tail length, bill length, tarsal length, and foot span (Earhart and Johnson 1970, Marti 1990, McGillivray 1987, Mueller 1986).

Between 1989 and 1992, we conducted research on two sympatric species, the Mottled Owl (*Ciccaba virgata*) and the Black-and-white Owl (*C. nigrolineata*), in Tikal National Park in Guatemala (Gerhardt 1991; Gerhardt *et al.* 1994a, 1994b). We studied the breeding biology, home range (Gerhardt *et al.* 1994b), and food habits (Gerhardt *et al.* 1994a) of these tropical owls, and recorded body mass and other measurements as we captured them. In this paper, we analyze those measurements with respect to dimorphism, and then discuss the implications of our findings upon various hypotheses regarding the causes and roles of RSD in owls.

METHODS

Trapping methods are described in Gerhardt *et al.* (1994b). All measurements were taken from breeding adult owls captured during the period beginning 1 month prior to egg-laying and ending at fledging of the young. Female body masses used in this analysis include only those taken during the nestling period. Owls were weighed to the nearest gram using a Pesola spring scale. Flattened wing chord and tail length (from insertion to tip) were measured to the nearest mm. Measurements are reported as means ± standard deviation. We applied to these measurements the dimorphism index (D.I.) devised by Storer (1966), D.I. = 100 (mean size of female - mean size of male) / 0.5 (mean size of female + mean size of male); we used the cube root of body mass to make the resulting index comparable to the indices of the linear measurements (Amadon 1943, Earhart and Johnson 1970). We also compared measurements between sexes using the Mann-Whitney "U" test (Siegel 1956), and applied Spearman rank correlations (Zar 1984) to size data from mated pairs to test for a linear relationship.

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We weighed eggs (to the nearest 0.5 g) within the first week after they were laid, and checked clutch sizes periodically (Gerhardt *et al.* 1994b). We assessed diet through analyzing pellets collected from under roosts and near nests, and from direct observation and prey remains in nests (Gerhardt *et al.* 1994a). The percentage of pellets containing parts of prey taxa are reported.

Data on North American owls used for comparison were taken from Earhart and Johnson (1970).

RESULTS

Female Mottled Owls (334.9 ± 22.0 g, N = 11) weighed significantly more than males (239.7 ± 13.3 g, N = 7; U = 77; $p < 0.001$). D.I. for (the cube root of) body mass was 12.05. Females also had significantly longer wing chords (24.6 ± 0.6 cm, N = 12 vs. 23.3 ± 0.6 cm, N = 8; U = 96, $p < 0.001$) and tails (15.0 ± 1.0 cm, N = 11 vs. 14.1 ± 0.6 cm, N = 7; U = 71, $p = 0.002$). Dimorphism indices for wing chord and tail length were 5.43 and 6.19, respectively.

The female Black-and-white Owl had a body mass of 535 g, a wing chord of 29.3 cm, and a tail length of 18.7 cm. Her mate had a body mass of 436 g, a wing chord of 28.6 cm, and a tail length of 16.5 cm. These data yield dimorphism indices of 6.81 (cube root of body mass), 2.42 (wing chord), and 3.13 (tail).

The dimorphism of body mass of these two species is compared graphically with those of North American owls in figure 1.

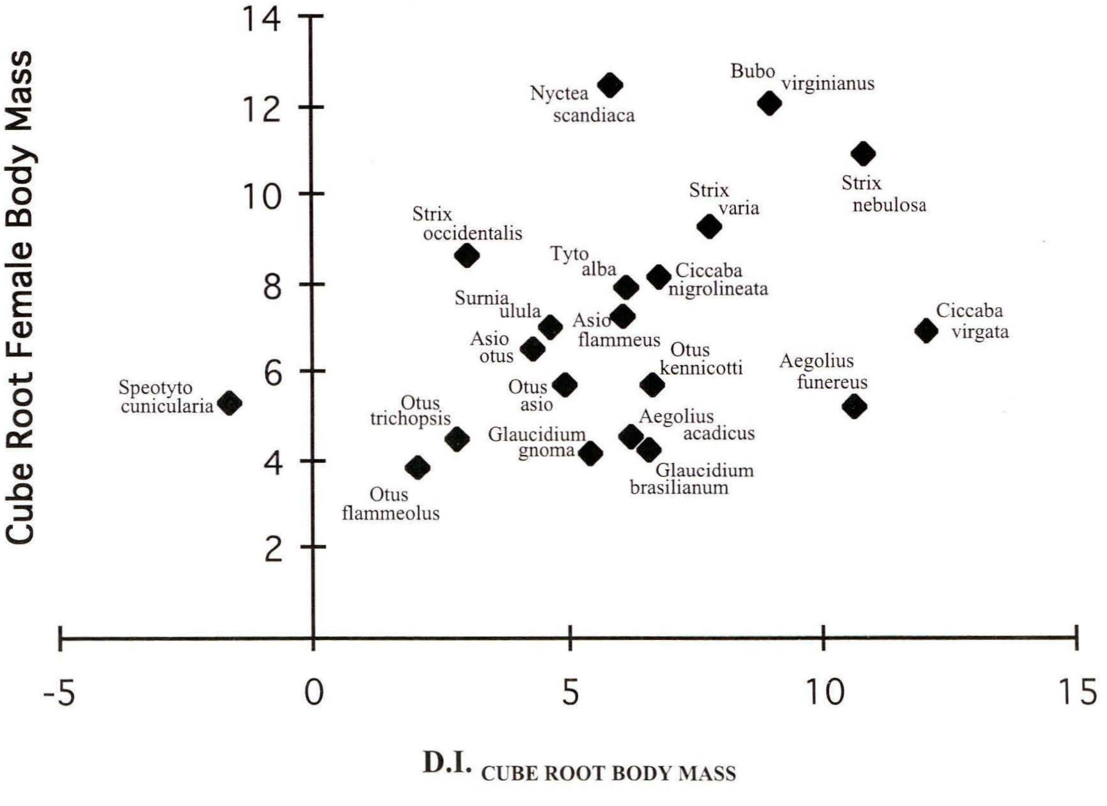

Figure 1.—*Cube root of female body mass vs. D.I.*$_{\text{CUBE ROOT OF BODY MASS}}$ *for North American owls and two* Ciccaba *owls.*

Mate choice in six pairs of Mottled Owls was not correlated with body mass ($r_s = -0.147$, $p > 0.5$) or wing chord ($r_s = -0.135$, $p > 0.5$), as no linear relationship existed for these measurements between mated birds.

Mean mass of Mottled Owl eggs was 28.2 ± 1.8 g (N = 16), and that of Black-and-white Owl eggs was 33.8 ± 2.3 g (N = 4). Mean clutch size for Mottled Owls was 2.2 ± 0.14 eggs (N = 13); each Black-and-white Owl clutch consisted of just one egg (N = 4) (Gerhardt *et al.* 1994b). Mottled Owl eggs and clutches weighed 8.4 percent and 18.5 percent of mean female body mass, respectively. Black-and-white Owl eggs (and, therefore clutches) weighed 6.3 percent of female body mass.

These two *Ciccaba* species differed in the mammalian component of their diets (Gerhardt *et al.* 1994a). Mottled Owls ate rodents, whereas Black-and-white Owls captured bats. Both species were highly insectivorous, however, and elytra and other hard beetle parts appeared in most pellets. Indeed, we observed other, more soft-bodied insects being eaten that were absent from pellets (and thus under-represented). Nonetheless, 98 percent of Mottled Owl pellets contained insect matter, and 44 percent contained only insect parts. Similarly, all Black-and-white Owl pellets contained insect parts, although 74 percent also contained some vertebrate remains (Gerhardt *et al.* 1994a). Figure 2 compares these two species, with respect to dimorphism and diet, with North American owls.

DISCUSSION

With respect to body mass, these Mottled Owls exhibited the most pronounced dimorphism yet documented among owls (fig. 1; Andersson and

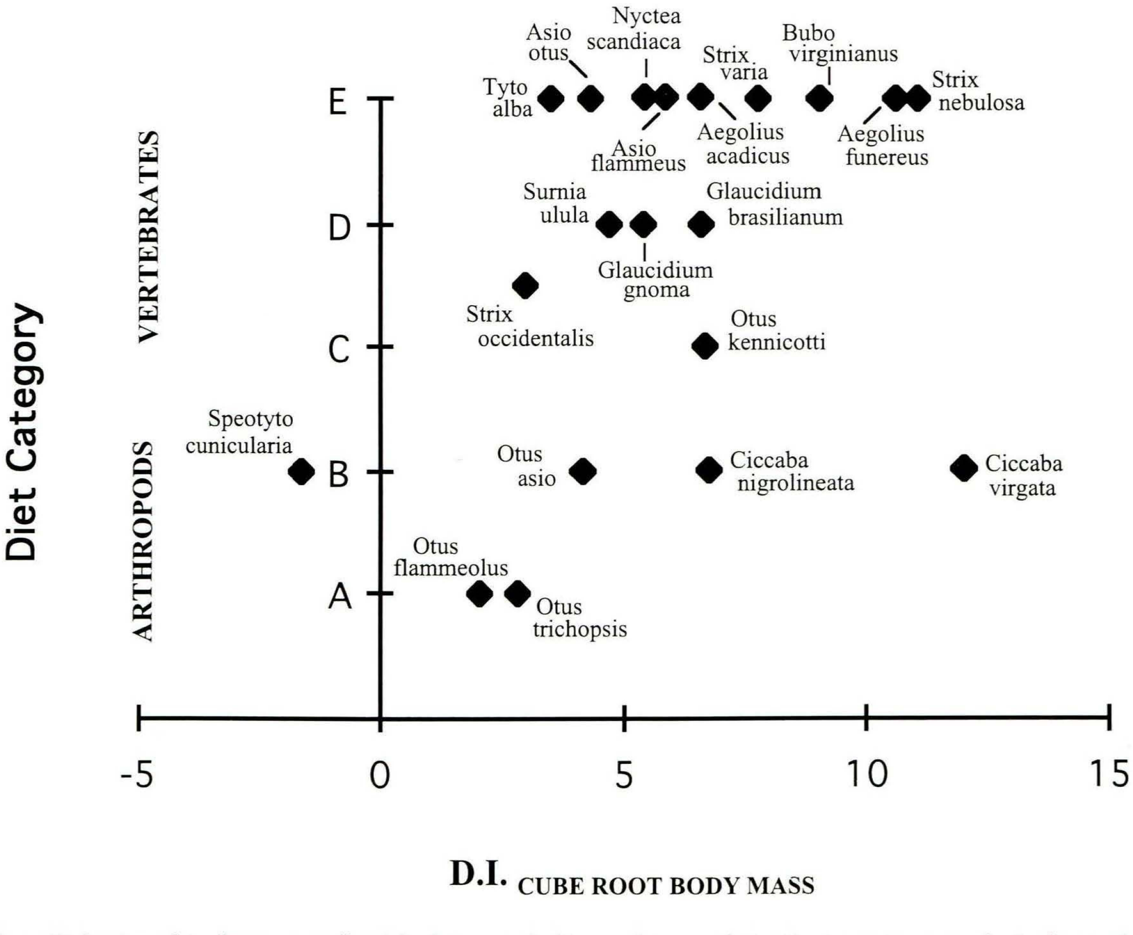

Figure 2.—*Relationship between food habits and dimorphism of North American owls (adapted from Earhart and Johnson 1970) with* Ciccaba virgata *and* C. nigrolineata *added. Diet categories are as follows: (A) feeds exclusively on arthropods; (B) primarily arthropods, few vertebrates; (C) arthtropods and vertebrates in equal numbers; (D) primarily vertebrates, few arthropods; (E) exclusively vertebrates.*

Norberg 1981, Earhart and Johnson 1970, Mueller 1986), with the possible exception of the European form of *Aegolius funereus*, Tengmalm's Owl (Lundberg 1986, Korpimäki 1986). Extent of weight dimorphism might have been less if body mass had been measured during the non-breeding season. Most hypotheses concerning the role and evolution of RSD are associated with aspects of breeding biology, however, and we agree with McGillivray (1987) that this is the most appropriate time for measuring body mass. Given that weights were taken during the breeding season, our results were conservative; we used female body masses only from the nestling period (higher values would likely have been obtained pre-laying and during incubation) and male masses from throughout the breeding season (male weights would likely have been lower had we used only nestling period values). Moreover, Mottled Owls ranked third among new-world owls in dimorphism of wing chords, behind only *Nyctea scandiaca* and *Aegolius funereus* (Earhart and Johnson 1970).

The mated pair of Black-and-white Owls was relatively dimorphic with respect to body mass (fig. 1) and tail length, but less so with respect to wing chord. In other pairs that we observed, but did not capture, a similar size difference was quite visible. We suspect that Black-and-white Owls probably exhibit significant size dimorphism, and that the extreme dimorphism exhibited by these Mottled Owls is not an anomaly among tropical owl species.

Although no body masses are given, Wetmore (1968) reports wing and tail measurements suggesting substantial RSD in *C. virgata*, *C. nigrolineata*, and the Pulsatrix Owls, but not in Lophostrix. Among African owls, RSD is clearly indicated by body masses reported for the African Wood Owl (*C. woodfordii*) and the eagle owl species *Bubo africanus*, *B. capensis*, *B. lacteus*, and *B. poensis* (Kemp 1987, Fry *et al.* 1988), whereas fishing owls of the genus Scotopelia are apparently monomorphic with respect to body mass (Fry *et al.* 1988).

Walter (1979) suggested that nesting in cavities inhibits the development of RSD. Our findings refute this idea, since Mottled Owls invariably nested in cavities (Gerhardt *et al.* 1994b). Similarly, an important prediction of the nest defense hypothesis (Andersson and Norberg 1981, Cade 1982, Reynolds 1972, Snyder and Wiley 1976, Storer 1966) is that, since cavity nests generally experience lower predation rates than open nests, cavity-nesting species should exhibit little dimorphism. Again, Mottled Owls bely this notion.

Proponents of the starvation hypothesis (Korpimäki 1986, Lundberg 1986) have used data primarily from European owl species to support their arguments. Simply stated, this hypothesis holds that larger females are better able to withstand harsh breeding season conditions, particularly in the early stages and at higher latitudes, and can incubate and brood longer during periods of poor or inconsistent prey deliveries by males. During 4 years of research in Guatemala, the harshest breeding season conditions were two consecutive nights of rain, with temperatures near 17° C. Moreover, during such conditions, prey remained abundant and active. If the starvation hypothesis accurately explains the role of RSD in European owls, it clearly does not do so for dimorphic tropical owls such as these *Ciccaba* species.

Researchers have tested whether mate choice is size-related in Barn Owls *Tyto alba* (Marti 1990) and Burrowing Owls *Speotyto cunicularia* (Plumpton and Lutz 1994), the latter being the only North American owl species in which males have larger body masses than females (Earhart and Johnson 1970). As in the Mottled Owls we examined, these studies concluded that mate choice was not influenced by size. It has been suggested (Marti 1990) that such findings refute the hypothesis that RSD evolved to facilitate female dominance in formation and maintenance of pair bonds (Amadon 1975, Cade 1982, Mueller 1986, Ratcliffe 1980, Smith 1982). We do not believe this to be the case. The evolution of RSD may be largely an accomplished process, in which case nearly all present-day individuals may fall within optimal size limits, and size may now be a less important factor in mate choice than other factors. The pair bond hypothesis remains an attractive one to us in that it would be equally applicable to tropical and temperate owls.

Three related hypotheses link RSD with relatively larger eggs (Cade 1982, Reynolds 1972, Selander 1972, von Schantz and Nilsson 1981), larger clutches (Mueller 1986), and more efficient incubation (Cade 1982, Snyder and Wiley 1976). That is, selection acts upon females, and favors larger size for reasons associated with egg-laying and incubation.

Mueller (1986) showed that a regression of egg mass upon female body mass had excellent predictive value, and found no correlation between RSD and the difference between observed and expected egg mass. Both Mottled Owls and Black-and-white Owls had egg masses much larger than those expected from the regression of data from North American owls (Mueller 1986), but it would be pointless to attempt to draw any conclusions from this fact. Rather, the point here is that, as with any hypothesis for the role of RSD, supporting arguments should be viewed as tentative and speculative until data on dimorphism and the associated trait, in this case egg mass, are available from the majority of owl species, most of which occur outside of the northern temperate zone.

The reproductive behavior of both *Ciccaba* species is in keeping with the trend among birds in general, in that tropical species have smaller clutches than ecologically similar or closely related temperate species (Lack 1966, Moreau 1944, Ricklefs 1969). That these *Ciccaba* owls also exhibit pronounced dimorphism is further evidence that facilitating larger clutches or more efficient incubation of clutches were not important causes of the evolution of RSD in owls.

Several hypotheses share the idea that RSD has evolved to allow members of a pair to capture different prey types or sizes (Andersson and Norberg 1981, Newton 1979, Reynolds 1972, Snyder and Wiley 1976, Storer 1966). These ideas enjoyed early popularity and, although more recent theorists (Korpimäki 1981, Lundberg 1986, Mikkola 1983, Mueller 1986, Mueller and Meyer 1985) have argued convincingly against prey-partitioning as a cause of RSD, these hypotheses remain in the conciousness when the subject of RSD arises. That the notion persists is exemplified by the following quote from Voous (1989): "Probably due to a rich supply of prey of different size, the Mottled Owl has apparently not needed to develop a noteworthy sexual dimorphism in size..." Taken as a whole, this statement appears to assume the validity of the prey-partitioning hypotheses. We have documented that the latter part of this statement is not true for the population that we studied. This is in spite of the fact that the first clause, that a rich supply of prey is available, is likely accurate. Data on the diets of temperate owls generally fail to show that the sexes within a species are in fact utilizing different prey types or sizes (Korpimäki 1981, Lundberg 1986, Mikkola 1983, Mueller 1986, Mueller and Meyer 1985). Rather, proponents of prey-partitioning hypotheses have argued that there is a positive correlation between RSD and percentage of vertebrate prey in the diet (Andersson and Norberg 1981, Earhart and Johnson 1970, Snyder and Wiley 1976) and that highly insectivorous owls exhibit relatively little dimorphism. The diet of these *Ciccaba* owls is at odds with this assumption, since both species are quite insectivorous and exhibit pronounced dimorphism (fig. 2). Whereas the positive correlation between RSD and percentage of vertebrate prey is the strongest, albeit indirect, argument for the prey-partitioning hypotheses, even this correlation is not supported with the inclusion of these tropical species.

Most discussions of the role and evolution of reversed size dimorphism in owls have had, naturally enough, a temperate zone bias. In some, there seems to be an underlying assumption that unstudied tropical owls neither exhibit pronounced dimorphism nor confound our favorite hypotheses. We have documented pronounced dimorphism in *Ciccaba virgata*, and have evidence for dimorphism in *C. nigrolineata* as well. This finding is at odds with basic assumptions or predictions of numerous hypotheses regarding the evolution of RSD. A gap clearly remains in our understanding of tropical owls; we believe that, as a corollary, a large gap remains in our understanding of the role and evolution of RSD in owls.

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LITERATURE CITED

Amadon, D. 1943. Bird weights as an aid in taxonomy. Wilson Bulletin. 55: 164-177.

Amadon, D. 1975. Why are female birds of prey larger than males? Journal of Raptor Research. 9: 1-11.

Amadon, D. 1977. Further comments on sexual size dimorphism in birds. Wilson Bulletin. 89: 619-620.

Andersson, M.; Norberg, R.A. 1981. Evolution of reversed sexual size dimorphism and role partitioning among predatory birds, with a size scaling of flight performance. Biological Journal of the Linnean Society. 15: 105-130.

Cade, T.J. 1960. Ecology of the Peregrine and Gyrfalcon populations in Alaska. Univ. Cal. Publ. Zool. 63: 151-290.

Cade, T.J. 1982. The falcons of the world. Ithaca, NY: Cornell University Press.

Earhart, C.M.; Johnson, N.K. 1970. Size dimorphism and food habits of North American owls. Condor. 72: 251-264.

Fry, C.H.; Keith, S.; Urban, E.K. 1988. The birds of Africa, Vol. 3. London, England: Academic Press.

Gerhardt, R.P. 1991. Response of Mottled Owls (*Ciccaba virgata*) to broadcast of conspecific call. Journal of Field Ornithology. 62: 239-244.

Gerhardt, R.P.; Gerhardt, D.M.; Flatten, C.J.; Bonilla G.N. 1994a. The food habits of sympatric *Ciccaba* owls in northern Guatemala. Journal of Field Ornithology. 65: 258-264.

Gerhardt, R.P.; Bonilla G.N.; Gerhardt, D.M.; Flatten, C.J. 1994b. Breeding biology and home range of two *Ciccaba* owls. Wilson Bulletin. 106: 629-639.

Kemp, A. 1987. The owls of southern Africa. London, Endgland: Struik Winchester.

Korpimäki, E. 1981. On the ecology and biology of Tengmalm's Owl (*Aegolius funereus*) in Southern Ostrobothnia and Suomenselkä, western Finland. Acta Universitatis Ouluensis Series A 118. Biol. 13: 1-84.

Korpimäki, E. 1986. Reversed size dimorphism in birds of prey, especially in Tengmalm's Owl *Aegolius funereus*: a test of the "starvation hypothesis." Ornis Scandinavica. 17: 326-332.

Lack, D. 1966. Population studies of birds. Oxford, England: Clarendon Press.

Lundberg, A. 1986. Adaptive advantages of reversed sexual size dimorphism in European owls. Ornis Scandinavica. 17: 133-140.

Marti, C.D. 1990. Sex and age dimorphism in the Barn Owl and a test of mate choice. Auk. 107: 246-254.

McGillivray, W.B. 1987. Reversed size dimorphism in 10 species of northern owls. In: Nero, R.W.; Clark, R.J.; Knapton, R.J.; Hamre, R.H., eds. Biology and conservation of northern forest owls: symposium proceedings; 1987 February 3-7; Winnipeg, MB. Gen. Tech, Rep. RM-142. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 59-66.

Mikkola, H. 1983. Owls of Europe. Vermillion, SD:Buteo Books.

Moreau, R.E. 1944. Clutch size: a comparative study, with special reference to African birds. Ibis. 86: 286-347.

Mueller, H.C. 1986. The evolution of reversed sexual dimorphism in owls: an empirical analysis of possible selective factors. Wilson Bulletin. 98: 387- 406.

Mueller, H.C.; Meyer, K. 1985. The evolution of reversed sexual dimorphism in size: a comparative analysis of the Falconiformes of the western Palearctic. Current Ornithology. 2: 65-101.

Newton, I. 1979. Population ecology of raptors. Vermillion, SD: Buteo Books.

Plumpton, D.L.; Lutz, R.S. 1994. Sexual size dimorphism, mate choice, and productivity of Burrowing Owls. Auk. 111: 724-727.

Ratcliffe, D. 1980. The Peregrine Falcon. Vermillion, SD: Buteo Books.

Reynolds, R.T. 1972. Sexual dimorphism in accipiter hawks: a new hypothesis. Condor. 74: 191-197.

Ricklefs, R.E. 1969. The nesting cycle of songbirds in tropical and temperate regions. Living Bird. 8: 165-175.

Selander, R.K. 1972. Sexual selection and dimorphism in birds. In: Campbell, B., ed. Sexual selection and the descent of man. 1871-1971. Chicago, IL: Aldine: 180-230.

Siegel, S. 1956. Nonparametric statistics for the behavioral sciences. New York, NY: McGraw-Hill.

Smith, S. 1982. Raptor "reverse" dimorphism revisited: a new hypothesis. Oikos. 39: 118-122.

Snyder, N.F.R.; Wiley, J.W. 1976. Sexual size dimorphism in hawks and owls of North America. Ornithological Monograph. 20: 1-96.

Storer, R.W. 1966. Sexual dimorphism and food habits in three North American accipiters. Auk. 83: 423-436.

von Schantz, T.; Nilsson, I.N. 1981. The reversed size dimorphism in birds of prey: a new hypothesis. Oikos. 36: 129-132.

Voous, K.H. 1989. Owls of the Northern Hemisphere. Cambridge, MA: M.I.T. Press.

Walter, H. 1979. Eleanora's Falcon: adaptations to prey and habitat in a social raptor. Chicago, IL: University of Chicago Press.

Wetmore, A. 1968. The birds of the Republic of Panama, Part 2. Misc. Coll., Washington, DC: Smithsonian, Vol. 150.

Zar, J.H. 1984. Biostatistical analysis. Englewood Cliffs, NJ: Prentice-Hall, Inc.

Habitat Selection of Northern Saw-whet Owls (*Aegolius acadicus brooksi*) on the Queen Charlotte Islands, British Columbia

Michael Gill and Richard J. Cannings[1]

Abstract.—The Northern Saw-whet Owl of the Queen Charlotte Islands, British Columbia is recognized as a distinct subspecies, *Aegolius acadicus brooksi*. Little is known of the biology of this subspecies, and no nests have ever been found. We surveyed for Northern Saw-whet Owls on the Queen Charlotte Islands between 4 May and 28 May, 1996 establishing 10 survey routes comprising a total of 238 survey stations on Graham and Moresby Islands. Routes were chosen to maximize coverage of different forest types. We detected 61 owls and identified five trees used by singing owls. No nests were found. We used discriminant function analysis to analyze general habitat variables collected at survey stations with or without owls in order to determine habitat preferences. Sites with owls were closer to riparian habitat and had more old forest (> 120 years old) and more young forest (10-30 years old) than sites without owls. Dominant tree species at sites did not have an effect on owl detections. Three trees used by singing owls were in old forest stands and two were in mature forest stands. These trees were larger in height and diameter, and had less shrub cover around them than randomly selected trees in similar aged forests.

The Northern Saw-whet Owl of the Queen Charlotte Islands, British Columbia is recognized as a distinct subspecies, *Aegolius acadicus brooksi* (Fleming). Little is known about this distinctive taxon, particularly regarding its habitat preferences and breeding biology, and no nest has ever been found. The Northern Saw-whet Owl is a cavity nester, and Cannings (1993) suggested that the species preferred older forests where snags were common, stating that "8 of 11 calling males found on the Queen Charlotte Islands in 1987 were in small pockets of old growth Sitka spruce in large areas of second-growth forest."

Because of its restricted range, its reliance on tree cavities, its apparent preference for old or mature forests, and the general lack of information about it, this subspecies has been placed on the British Columbian Ministry of Environment's Blue List of vulnerable taxa. This study was designed to discover some basic information about the distribution, populations and habitat associations of the Queen Charlotte Northern Saw-whet Owl.

METHODS

Study Area and Site Descriptions

Queen Charlotte Islands

The Queen Charlotte Islands (fig. 1) lie about 100 km off the coast of British Columbia in a region of high rainfall (2 to 5 m annually) and moderate temperatures. The islands are covered in coniferous rainforests, with the dominant tree species being western hemlock (*Tsuga heterophylla* (Rafinesque)), western redcedar (*Thuja plicata* Donn), Sitka spruce (*Picea sitchensis* (Bongard)), lodgepole pine (*Pinus contorta* Douglas), yellow cedar (*Chamaecyparis nootkatensis* (D. Don))and red alder (*Alnus rubra* Bongard).

Survey Routes

We established 10 survey routes along roads on Graham and Moresby Islands comprising a total

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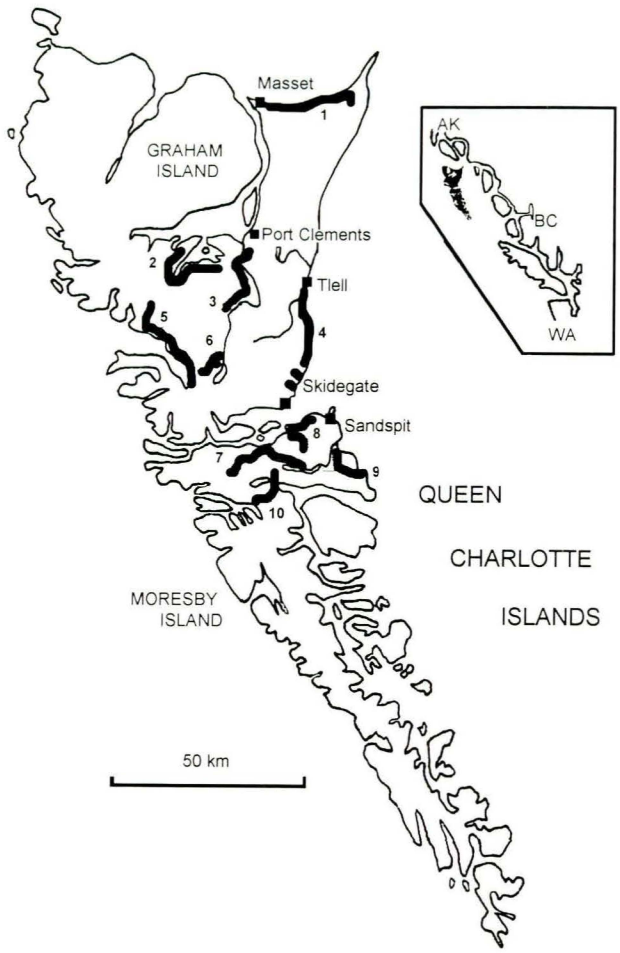

Figure 1.—*The Queen Charlotte Islands, British Columbia, showing the 10 survey routes (thick grey lines) covered in the study: 1, Tow Hill; 2, Datlamen Main; 3, Yakoun Main; 4, Tlell; 5, Rennell Sound; 6, Rennell Main; 7, Deana West; 8, Alliford Bay; 9, Gray Bay; 10, Peel Inlet.*

of 238 survey stations located 1 km apart (fig. 1). We chose survey routes in an attempt to maximize coverage of different forest stand types, biogeoclimatic subzones, and elevations. At each site we noted the following variables: elevation, biogeoclimatic subzone distance to salt water and distance to riparian zone. Within a 500-m diameter area around the survey site, we estimated the percentage cover of five different forest stand types (see below), and ranked tree species by forest cover dominance.

Forest Stand Types

We defined five categories of forest stand types (adapted from Hayward *et al.* 1993) allowing for simple translation from the different forest cover maps provided by the forest companies and the British Columbian Ministry of Forests. The five forest stand classes were:

0 Clearcut; essentially barren land; 0-10 years after initial disturbance.

1 Young forest; few or no seed producing trees, where seedling establishment is common and leaf area is increasing; 10-30 years of age.

2 Aggradation stage forest; tree establishment is significantly reduced and competition has resulted in tree mortality, but stand structure is primarily a result of the major disturbance. Trees of a single age class, new snags and few seedlings; 30-60 years of age.

3 Mature forest; mortality and regeneration are prominent processes and regeneration results from parent trees; tree-fall gaps and uneven tree diameter distribution; 60-120 years of age.

4 Old forest; a stand whose age and physical structure is currently influenced by processes within the stand; wide variety of tree sizes and ages and a patchy structure; 120+ years of age.

Of the total area surveyed, 17 percent was occupied by clearcuts, with 14 percent young forest, 28 percent aggradation stage forest, 18 percent mature forest, and 23 percent old forest.

Biogeoclimatic Subzones

Almost all of the Queen Charlotte Islands lie within the Coastal Western Hemlock (CWH) biogeoclimatic zone (Meidinger and Pojar 1991). Three subzones and variants (Green and Klinka 1994) occurred within the study area: 209 survey sites were in the Submontane Wet Hypermaritime subzone (CWH wh1), 4 were in the Montane Wet Hypermaritime subzone (CWH wh2), and 25 in the Rennell Sound area were in the Central Very Wet Hypermaritime subzone (CWH vh2).

Surveys

We began surveys as soon as possible after dark and continued for approximately 5 hours. We conducted the call surveys from roads, driving for 1 km, stopping, listening for 2 minutes for unsolicited song, playing a recording of owl song for 1 minute, then listening for 1 minute. The playback/listening section was repeated two more times if no owls responded to the first. If an owl was heard singing unsolicited before tape playback began, we attempted to walk into the site to locate the song tree. We mapped owl positions through triangulation whenever possible. We began the surveys on the 4th of May and completed them on the 28th of May, and surveyed all 10 routes twice. On the second survey we did not play tape recordings at sites that produced owls on the first survey. We also searched for nests in areas where owls were found.

Song Trees

We attempted to approach all owls heard singing unsolicited by our calls in order to locate the tree they were singing from (song tree). We did a more detailed habitat analysis in 20-m square plots around these trees, and compared these data with similar tree-centered plots taken at 39 randomly located trees in similar forest types. At each of these plots we collected the following data: elevation, biogeoclimatic subzone, distance to salt water, distance to riparian zone, distance to ecotone, distance to clearcut, forest stand class, slope, aspect, percent shrub coverage, dominant shrub species, canopy closure (measured with a spherical densiometer), coarse woody debris volume (estimated visually), snag density (measured along a 100 m x 20 m transect), and the species, height and diameter-at-breast-height (d.b.h.) of all trees within the plot. We also noted the species, profile (healthy, diseased, dead), height and d.b.h. of the song tree or randomly selected tree at the center of the plot.

Statistical Analysis

Survey Sites

Due to non-normal data distributions, we employed Mann-Whitney U-tests to test the equality of the mean values of the habitat measurements for survey sites with and without owls. Although each of the univariate tests can indicate Northern Saw-whet Owl habitat preferences, a multivariate analysis was used to analyze the habitat relationships as a combination of interrelated variables.

Discriminant function analysis was used to reveal the measures that had the most influence in discriminating points with and without owls (Manly 1986). Canonical discriminant function analysis using Mahalanobis distance as the selection criteria, was used to produce a discriminant function to test that function's ability in separating the two groups (SAS 1993). This function is the best linear artificial variable for separating the groups. Such an analysis requires quantitative, multivariate normal distributions with uncorrelated variables. As a result, only normally distributed, quantitative variables showing little correlation with the other variables were chosen.

A Pearson correlation was performed for all pairwise combinations of habitat variables. None of the variables were highly correlated ($r < 0.70$). As all variables were non-normal, we square-root transformed the data (SQR(X + 0.5)) in order to achieve normality for each quantitative variable. When a Pearson pairwise correlation was performed on the transformed variables, distance to salt water and elevation were strongly correlated ($r = 0.710$). As these were the only two variables to be strongly correlated, all eight of the quantitative variables (elevation, distance to salt water, distance to riparian, class 0, class 1, class 2, class 3, and class 4) were retained for the discriminant analysis.

This process resulted in eight variables remaining for the discriminant function analysis. We allowed for prior probabilities of group membership for the discriminant analysis. The equality of the discriminant scores, and thus, the effectiveness of the linear equation was determined by the Wilks' Lambda F-statistic. A cross-classification procedure (SAS 1993) using these linear discriminant equations was used to assess their accuracy in correctly classifying the survey points.

Canonical discriminant analysis produced pooled within-class standardized canonical coefficients and pooled within canonical structure coefficients. The standardized coefficient provides a measure of a variables relative contribution to the overall classification (SAS 1993). The structure coefficient determines the correlation between the variables and the function, providing a relative measure of the specific variable's ability to discriminate between the two groups (SAS 1993). To simplify the analysis, we chose variables with high standardized and structure coefficients to produce canonical discriminant functions with various combinations of these variables. These functions were then assessed for their accuracy in classifying the data. The most accurate function with the fewest number of variables was then chosen as the most effective and efficient function for separating points with and without owls.

Song Trees

We employed two sample t-tests and Mann-Whitney U-tests (Wilkinson 1992) to compare mean values of the quantitative variables with normal and non-normal distributions, respectively. As the sample size of song trees was small and, thus, power of analysis limited, multivariate analysis was not employed. Mean d.b.h. and height by tree species was calculated for each group and compared using two-sample t-tests (Wilkinson 1992). Mean number of trees per hectare by species and mean number of total stems per hectare was recorded for both groups and compared using two-sample t-tests (Wilkinson 1992).

RESULTS

We recorded 44 individual Northern Saw-whet Owls during the first round of surveys and 17 on the second round of surveys for a total of 61 individual owls. We located only five song trees and were unable to find any nests.

Owls were detected at points closer to riparian habitat with greater amounts of class 1 and class 4 forest (table 1). The other variables (elevation, distance to salt water, and amounts of class 0, class 2, and class 3 forest) did not have an influence on owl detection at the points surveyed (table 1). We detected owls with greater frequency in the CWHvh2 biogeoclimatic subzone than in the other two subzones (table 2). Neither the dominant tree species nor combinations of the two most dominant tree species had an effect on owl detections (tables 3 and 4).

Table 1.—*Comparison of means and standard errors for survey points with and without Northern Saw-whet Owls* (Aegolius acadicus), *Queen Charlotte Islands, British Columbia.*

Habitat variable[1]	Owls absent (n=188)		Owls present (n=58)		P-value[2]
	Mean	S.E.	Mean	S.E.	
Percent of Class 0	17.03	1.94	17.10	3.75	0.736
Percent of Class 1	12.30	1.99	20.30	3.86	0.078
Percent of Class 2	29.79	2.75	21.80	5.31	0.238
Percent of Class 3	19.87	2.26	10.10	4.37	0.111
Percent of Class 4	21.02	2.25	30.70	4.34	0.047
Elevation (m)	75.54	7.22	89.90	13.97	0.305
Distance to Riparian (m)	572.60	63.83	302.20	123.44	0.025
Distance to Salt Water (km)	2.36	0.22	2.45	0.43	0.468

[1] See methods for definitions.

[2] P-values are from Non-parametric Mann-Whitney U-tests (Wilkinson 1992).

Table 2.—*Mean number of Northern Saw-whet Owls* (Aegolius acadicus) *detected per survey point within each biogeoclimatic zone, Queen Charlotte Islands, British Columbia. Biogeoclimatic zone had a significant effect on owl detection (ANOVA (Wilkinson 1992), F = 4.622, N = 238, P = 0.011).*

Biogeoclimatic zone	Mean	S.E.	Sample size
CWHvh2	0.440	0.080	25
CWHwh1	0.182	0.028	209
CWHwh2	0.250	0.201	4

Table 3.—*Mean number of Northern Saw-whet Owls (*Aegolius acadicus*) detected per survey point by dominant tree species, Queen Charlotte Islands, British Columbia. Dominant tree species did not have a significant effect on owl detections (ANOVA (Wilkinson 1992), F = 0.102, N = 233, P = 0.959).*

Dominant tree	**Mean**	**S.E.**	**Sample size**
Sitka spruce	0.196	0.041	97
Western redcedar	0.211	0.054	57
Western hemlock	0.224	0.050	67
Red alder	0.167	0.118	12

Table 4.—*Mean number of Northern Saw-whet Owls (*Aegolius acadicus*) detected per survey point for forest dominated by different combinations of tree species, Queen Charlotte Islands, British Columbia. Pairs of dominant tree species had no effect on owl detections (ANOVA (Wilkinson 1992), F = 0.672, N = 187, P = 0.645).*

Dominant tree species (First, Second)	**Mean**	**S.E.**	**Sample size**
Sitka spruce, western hemlock	0.188	0.050	64
Western redcedar, western hemlock	0.250	0.063	40
Western hemlock, western redcedar	0.200	0.068	35
Western hemlock, sitka spruce	0.192	0.079	26
Western redcedar, sitka spruce	0.000	0.127	10
Sitka spruce, western redcedar	0.250	0.116	12

Discriminant function analysis of the eight quantitative, transformed variables produced a linear model which was not satisfactory in separating the groups (Wilks' Lambda F-statistic = 1.661, n = 238, P = 0.109, SAS 1993). This linear discriminant function was only able to correctly classify 59.7 percent (142 of 238) of the survey points. This function revealed that owl presence was most influenced by proportion of class 4 forest, proportion of class 1 forest, and distance to riparian habitat (table 5). A linear discriminant equation employing these three variables produced an effective linear model (Wilks' Lambda F-statistic = 4.117, P = 0.007, n = 238, SAS 1993) that was still only able to correctly classify 59.7 percent (142 of 238) of the survey points into their respective groups. Other combinations of these three variables could not produce a more effective and efficient linear model.

Tree-centered Habitat Analysis

We were able to locate only five song trees; two were in mature forest and three were in old forest. To narrow our comparison, we restricted our randomly sampled trees to mature and old forests. Owl song trees were associated with significantly lower shrub coverage and a greater canopy closure than generally found in class 3 and class 4 forests (table 6). Owls were selecting song trees that were greater in height and d.b.h. than what is generally available in these forests (table 6). Song trees were found in areas with significantly smaller-diameter western redcedar and with taller western hemlocks than what was usually found in these forests (table 7 and 8). Although total tree densities did not differ surrounding song trees and random trees, there were significantly lower densities of Sitka spruce trees surrounding song trees (table 9). Song tree species and profile were not significantly different from those of randomly-selected trees.

DISCUSSION

The results from the habitat analysis of survey sites show an interesting combination of habitat associations for Queen Charlotte Northern Saw-whet Owls, that of older forests next to very young forests. Old forests may be attractive to

Table 5.—*Standardized coefficients produced by canonical discriminant function analysis for points with and without Northern Saw-whet Owls* (Aegolius acadicus), *Queen Charlotte Islands, British Columbia.*

Discriminant function variable	Structure coefficient	Standardized coefficient
Elevation	0.266	-0.071
Distance to riparian	-0.602	-0.558
Distance to salt water	0.136	-0.056
Class 0	0.066	0.516
Class 1	0.495	0.946
Class 2	-0.312	0.458
Class 3	-0.479	0.412
Class 4	0.542	0.975

Table 6.—*Comparison of means and standard errors for Northern Saw-whet Owls* (Aegolius acadicus) *song trees and randomly selected trees, Queen Charlotte Islands, British Columbia.*

Habitat variable	Singing trees			Random trees			
	Mean	S.E.	N	Mean	S.E.	N	P-value
Elevation (m)	84.0	32.8	5	71.5	14.3	39	0.741[1]
Distance to salt water (km)	5.3	4.8	5	14.7	12.8	39	0.052[2]
Distance to riparian (m)	127.0	32.5	5	433.3	125.3	39	0.985[2]
Distance to ecotone (m)	196.0	87.2	5	331.9	80.7	39	0.273[1]
Distance to clearcut (m)	406.0	171.1	5	3,899.8	1,271.7	33	0.476[2]
Slope (deg)	6.0	6.0	5	7.2	2.0	39	0.569[2]
Aspect (deg)	244.0	—	1	168.5	28.2	14	n/a
Shrub coverage (percent)	0.4	0.2	5	30.5	6.3	39	0.016[2]
Canopy closure (percent)	98.8	0.6	5	93.3	1.5	39	0.002[1]
Coarse woody debris vol (m^3)	12.8	2.3	5	12.0	1.4	39	0.775[1]
Snag density (1/ha)	34.4	3.9	5	33.9	3.7	39	0.934[1]
Tree height (m)	48.2	8.0	5	23.7	1.8	39	0.037[1]
Tree d.b.h. (cm)	167.7	32.8	5	44.0	4.0	39	0.019[1]

[1] P-values resulting from two-sample t-tests with separate variances.

[2] P-values resulting from non-parametric Mann-Whitney U-tests (Wilkinson 1992).

Table 7.—*Mean diameter of each tree species found within random and Northern Saw-whet Owls* (Aegolius acadicus) *song tree plots, Queen Charlotte Islands, British Columbia.*

Tree species	Singing tree plots			Random plots			P-value[1]
	Mean	S.E.	N	Mean	S.E.	N	
Lodgepole pine	36.8	2.7	4	45.3	8.2	4	0.386
Red alder	—	—	—	33.9	3.0	16	n/a
Sitka spruce	49.1	5.3	6	38.1	1.9	152	0.097
Western hemlock	35.9	2.3	56	32.0	1.0	294	0.137
Western redcedar	32.9	3.0	8	46.0	2.1	184	0.003
Yellow cedar	—	—	—	37.1	4.7	27	n/a

[1] P-values resulted from two-sample t-tests with separate variances (Wilkinson 1992).

Table 8.—*Mean height for each tree species found within random and Northern Saw-whet Owls (*Aegolius acadicus*) song tree plots, Queen Charlotte Islands, British Columbia.*

Tree species	**Singing tree plots**			**Random plots**			**P-value**[1]
	Mean	**S.E.**	**N**	**Mean**	**S.E.**	**N**	
Lodgepole pine	31.8	1.7	4	29.3	0.9	4	0.249
Red alder	—	—	—	18.8	1.6	16	n/a
Sitka spruce	33.8	3.3	6	27.4	0.8	152	0.109
Western hemlock	26.8	1.2	56	22.3	0.6	294	0.001
Western redcedar	24.9	1.7	8	24.6	0.7	184	0.896
Yellow cedar	—	—	—	21.0	1.4	27	n/a

[1] P-values from two-sample t-tests with separate variances (Wilkinson 1992).

Table 9.—*Mean number of trees by species per hectare, measured from plots around five Northern Saw-whet Owls (*Aegolius acadicus*) song trees and 39 randomly selected trees in similar forest types, Queen Charlotte Islands, British Columbia.*

Tree species	**Singing tree**		**Random tree**		**P-value**[1]
	Mean	**S.E.**	**Mean**	**S.E.**	
Lodgepole pine	20.0	20.0	2.6	1.5	0.433
Red alder	0.0	0.0	10.3	3.8	n/a
Sitka spruce	30.0	15	97.5	25.0	0.023
Western hemlock	280.0	58.8	182.1	22.0	0.139
Western redcedar	40.0	34.1	117.9	29.8	0.111
Yellow cedar	0.0	0.0	17.3	7.5	n/a
Total stems	375.0	51.2	429.5	40.8	0.424

[1] P-values resulting from two-sample t-tests using separate variances.

the owls, since they need cavities for nesting and an open understory for hunting. Young forests may provide good roosting habitat, since this species roosts in thick vegetation, either near the ends of branches on large trees or near the trunks of small, densely growing trees (Cannings 1993). It is difficult to explain the high frequency of owl encounters in the CWH vh2 biogeoclimatic subzone. Only 25 survey sites, all on one survey route, were in this subzone, so other factors working at a larger scale could have affected owl numbers there.

The finding that song trees were relatively close to salt water might be due to some unknown topographic variable, such as the frequency of canyons that might have prevented us from reaching song trees in areas farther from the sea. Data from song trees did not support the survey results that owls were associated with riparian zones. The fact that song trees were significantly larger than randomly selected trees would suggest that the owls might be using high song posts to broadcast their songs as far as possible through the dense forests. Although the sample size for song trees is low, the variances on the measurement means were small, indicating that this was a habitat feature the owls were selecting.

While the results of this study identify habitat associations of Northern Saw-whet Owls on the Queen Charlotte Islands, there are several factors that may have affected the results. One is the time of year the surveys were done. The seasonal phenology of owl activity on the Queen Charlottes is poorly known. Conducting surveys in March or April, when owl singing activity peaks in other parts of the species' range (Cannings 1993), might increase the number of owl encounters as well as reduce the chance that birds encountered were those in suboptimal habitat that had been unable to attract mates early in the season.

Finding song trees depended on getting to them promptly in the dark. The main reasons for not reaching some were the presence of deep canyons and early cessation of song.

Perhaps the biggest bias facing the data analysis and interpretation is that of depending on playback response to get habitat association data in a patchy environment. The Queen Charlotte Islands is covered with a patchwork of forest stand types, the result of clearcut logging practices over the last few decades. The habitat mix within 500 m of a survey site may not accurately represent the habitat types used by birds called into that site. Our plans to find unsolicited singing locations were designed to avoid this problem, as was done for Boreal Owls (Herren *et al.* 1996). Unfortunately this was difficult and data were too few to perform a useful multivariate analysis.

There is still a need for more research on this topic. Field work should begin in late March or early April, and should concentrate on finding song trees and nest sites. Radio telemetry would provide more accurate data on this owl's habitat needs.

ACKNOWLEDGEMENTS

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LITERATURE CITED

Cannings, Richard J. 1993. Northern Saw-whet Owl, In: Poole, A.; Stettenheim, P.; Gill, F., eds. The birds of North America, No. 42. Philadelphia, PA: The Academy of Natural Sciences; Washington, DC: The American Ornithologists' Union.

Green, R.N.; Klinka, K. 1994. A field guide to site identification and interpretation for the Vancouver Forest Region. Victoria, BC: British Columbian Ministry of Forests, Research Program. 285 p.

Hayward, G.D.; Hayward, P.H.; Garton, E.O. 1993. Ecology of Boreal Owls in the northern Rocky Mountains, USA. Wildlife Monographs. 124.

Herren, Vicki; Anderson, Stanley H.; Ruggiero, Leonard F. 1996. Boreal Owl mating habitat in the northwestern United States. Journal of Raptor Research. 30: 123-129.

Manly, B.F.J. 1986. Multivariate statistical methods - a primer. New York, NY: Chapman and Hall. 159 p.

Meidinger, Del; Pojar, Jim. 1991. Ecosystems of British Columbia. Victoria, BC: British Columbian Ministry of Forests. 330 p.

SAS Institute. 1993. SAS/ETS user's guide: version 6. Cary, NC: SAS Institute. 1,022 p.

Wilkinson, L. 1992. Systat for Windows: statistics, version 5 ed. Evanston, IL: Systat, Inc. 750 p.

Matrix Population Models as a Tool in Development of Habitat Models

Gregory D. Hayward and David B. McDonald[1]

Abstract.—Building sophisticated habitat models for conservation of owls must stem from an understanding of the relative quality of habitats at a variety of geographic and temporal scales. Developing these models requires knowing the relationship between habitat conditions and owl performance. What measure should be used to compare the quality of habitats? Matrix population models represent a powerful tool to aid in designing habitat research. Through sensitivity and elasticity analysis we can identify the demographic transitions most important in determining population growth. Matrix methods also provide a powerful method for assessing individual fitness in varying environmental conditions. Matrix models can help us decide how to: (1) focus field efforts toward measuring the most important demographic parameters, and (2) focus on those habitat characteristics with the greatest effect on population dynamics.

Models of owl habitat relationships rely on information describing the association between owl species and measurable habitat characteristics. An ideal habitat model will rank the relative quality of habitats at one or more spatial and temporal scales. Developing such a ranking system requires evaluation of the performance of individuals or populations in a variety of habitats. Designing such studies is not trivial (e.g., see review in Morrison *et al.* 1992). Along with the problems of sampling owl performance at the appropriate range of temporal and spatial scales, and of replicating samples, a measure of 'performance' must be chosen. What metric measure should be used to compare the quality of habitats?

Biologists studying habitat associations of various vertebrate taxa employ a wide range of metrics. Relative comparisons of habitat use vs. availability of habitat are common (see examples in Alldredge and Ratti 1986). In other studies population density, reproductive rate, measures of body condition, or less frequently, survival rates are used to compare habitats (e.g., Morrison *et al.* 1992, VanHorne 1983). The choice of metrics is often determined largely by logistical and sampling constraints. We suspect, however, that the choice of metrics is often made without rigorous consideration of the relative value of different measures of performance. Some biologists contend that comparison of individual fitness among habitats would provide the ideal metric to ultimately rank habitat quality.

We propose that measures derived from population matrix models (Caswell 1989, McDonald and Caswell 1993) provide flexible, powerful and intuitively appealing metrics with rigorous links to fundamental theory in population ecology and genetics. The metrics include many of those listed above, including measures of individual fitness (McGraw and Caswell 1996) and population growth. They also include rigorous sensitivity analyses that point to the most critical life history transitions and allow comparison among populations or habitats that vary in one or more important ways. The models readily incorporate stochastic features and density dependence, and are especially useful when data are incomplete. Much of the output is robust to non-equilibrium conditions and populations can be classified by age or stage (e.g., breeder versus floater) to incorporate the most biologically meaningful aspects of the life history. The methods therefore provide an important tool to guide future efforts in research and management.

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DESCRIPTION OF THE BASIC MODELING FRAMEWORK

Matrix population models can classify life cycles either by age or stage. Age-classified models examine population dynamics by dividing the continuous age variable into discrete age classes, each of the same duration. Stage-classified models are more flexible, and accommodate analysis of more complex life cycle patterns. The stages may describe social status (e.g., breeder versus floater), developmental stages, or spatial locations (e.g., high-quality versus low-quality territory). Transitions among the stages are governed by **vital rates** that describe processes such as growth, fertility, survival or even the probability of becoming a breeder or obtaining a high-quality territory.

Matrix population models were initially developed by Leslie (1945, 1948). Caswell (1989) provided a comprehensive and synthetic overview of the modeling framework, and McDonald and Caswell (1993) provided a briefer review of their application to avian studies. Matrix models are the basis for several computer packages for population and viability analysis (e.g., RAMAS). As a supplement to the computer-based matrix analyses, life cycle graphs provide a powerful and intuitively appealing tool for model development. We begin with a brief introduction to age- and stage-classified models and then provide an example to illustrate its application to questions related to the habitat, conservation, and population dynamics of owls.

Age-classified Models

Age-classified models place estimates of fertility and survival rates in a square 'projection matrix'. In the simplest case (Leslie matrix) the top row of the projection matrix represents age-specific fertility, while the subdiagonal represents age-specific survival. A common extension is to add an element at the lower right that represents survival of 'adults' (the term in fig. 1). The remaining elements of the projection matrix are zero.

The corresponding life cycle graph (fig. 2) is mathematically equivalent to the matrix but provides a more intuitively appealing version of the life cycle. In the life cycle graph, circles (called **nodes**) represent stages or states. Arrows (called arcs or loops) connecting the

(a)

$$\begin{bmatrix} F_1 & F_2 & F_3 \\ G_{21} & & \\ G_{31} & P_2 & P_3 \end{bmatrix}$$

(b)

$$\begin{bmatrix} .04 & .31 & .53 \\ .20 & & \\ .03 & .46 & .46 \end{bmatrix}$$

Figure 1.—*(a) A Leslie matrix with three age classes—first-year birds, second-year birds, and 'adults'. The P_x represent survival rates from one age class to the next. F_x represents the fertility of females at age x, and is a compound term given by the product of the number of offspring, M_x, and the survival of females from the post-breeding census to the next breeding pulse (P_x). If we conducted a pre-breeding census, the parameterization would be slightly different (see McDonald and Caswell 1993). For most bird studies it is more convenient to conduct post-breeding censuses, using the number of fledglings as the count for 'first-year' birds.*

(b) A numerical example of using the matrix in figure 1a to 'project' the population at time t + 1 ('projected' census vectors to the right of the equal sign) from the population at time t (census vector to the right of the matrix). At time t there were 52 first-year owls (fledglings), 16 second-year birds (just past their first birthday) and 32 'adults'. At time t + 1 we therefore expect 55 fledglings, 17 second-year birds, and 34 'adults'. The population growth rate, λ, for this example is 1.06.

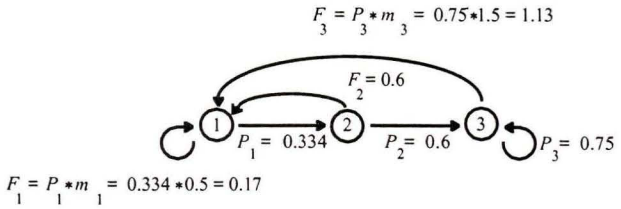

F_3 = P_3 * m_3 = 0.75*1.5 = 1.13
F_2 = 0.6
1
2
3
P_1 = 0.334
P_2 = 0.6
P_3 = 0.75
F_1 = P_1 * m_1 = 0.334 *0.5 = 0.17

Figure 2.—*A life cycle graph corresponding to the Leslie matrix given in figure 1a. The circles (nodes) represent the three age classes, while the arrows (arcs) represent the vital rates—survival and fertility, as given in figures 1a and 1b. The self-loop on Node 3 (P_3 = 0.75) represents the survival rate of 'adult' females. For more complex life cycles, the graph is very useful in formulating the model from which a matrix can be constructed for computer analysis.*

nodes represent the vital rates (transitions between states). In figure 2, Nodes 1 and 2 represent first-year and second-year individuals, respectively, while Node 3 represents 'adult' individuals. Parameter estimates for transition rates are represented by P_x — indicating survival rate from stage or age class x to $x + 1$, and F_x — indicating the mean number of female offspring produced by females of age x, m_x, times the probability, P_x, that a female of age class x (censused just after the breeding season) will survive from that census until the next breeding pulse, just before the annual census. 'Adult' survival is represented by an arc called a 'self-loop', P_3, that represents the (survival) probability of returning to the 'adult' stage at the next census.

From this simple representation of the population vital rates we can calculate a number of useful demographic parameters (table 1). Figure 1b shows hypothetical values for the matrix

Table 1.—*Demographic metrics obtained from analysis of a population matrix,* **A**, *with elements* a_{ij} *representing the transitions from st(age) j to (st)age i.*

Parameter	Derivation	Importance
Growth rate (λ)	Dominant eigenvalue of **A**	Finite rate of increase; can be developed as measure of individual fitness.
Sensitivity (s_{ij})	$\partial\lambda/\partial a_{ij}$ (partial derivative of λ with respect to a_{ij})	Sensitivity of λ to a change in a one of the vital rates (a_{ij}); directly equivalent to a selection gradient in quantitative genetics.
Elasticity (e_{ij})	$s_{ij} * a_{ij}/\lambda$	Proportional sensitivity of λ to a change in one of the a_{ij}.
Stable (st)age distribution	Right eigenvector	Proportion of population in each (st)age.
Reproductive value	Left eigenvector	Value of an individual of a given (st)age as a seed for population growth.
Cohort generation time (μ_1)	(Caswell & McDonald 1993)	Mean age of reproduction for a cohort.
Age of stage	(Cochran & Ellner 1992)	Mean and variance for age of individuals in a given stage. (used for stage-classified models)
Damping ratio	Second eigenvalue of **A**	Measures rate at which damped oscillations return the population to equilibrium.

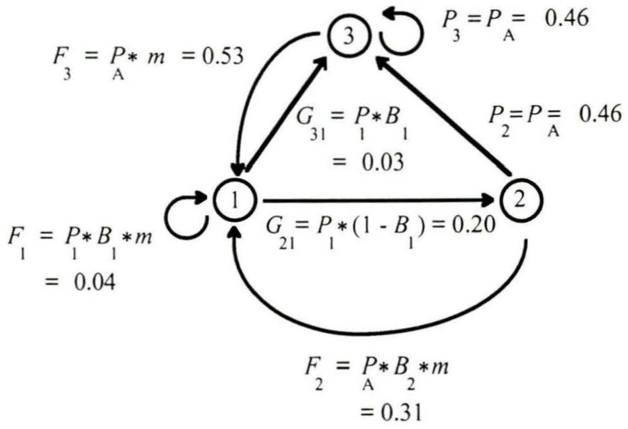
elements and 'projects' the expected census vector at time $t + 1$ from the census at time t. Because λ (=1.06) is slightly greater than one, the number of individuals at time $t + 1$ is slightly greater than at time t. Important assumptions underlying the simple Leslie matrix model are absence of density dependence and constancy of the age-specific vital rates.

Age-classified models have several limitations. For long-lived organisms, matrix truncation or the adult survival self-loop (fig. 2) may affect some aspects of the results (see McDonald and Caswell 1993, p. 166). For example, senescence is not well modeled by either abrupt truncation or a self-loop for 'adult' survival. Although senescence has long been ignored as a demographic feature of avian populations, recent analyses indicate that it may be an important feature of avian population dynamics (McDonald *et al.* 1996). A more important drawback of simple age-classified models is that age may not be the most appropriate basis for assessing population dynamics. For example, individuals of the same age that differ in reproductive status (e.g., breeders versus floaters) will have very different demographic outputs. Such life cycles are better analyzed with stage-classified models that capture the most biologically important transitions.

Formulating a Stage-classified Model

Stage structured models overcome some of the shortcomings of the age-classified models. In particular, complex social dynamics or breeding systems can be modeled and analyzed with these models. Caswell (1989) and McDonald and Caswell (1993) describe formulation and analysis of stage-classified models and provide examples for taxa with a variety of life cycles. As a first step in formulating a stage-classified model, the life cycle graph is particularly important and useful.

We illustrate the development of a stage-classified model by describing one possible life cycle graph (fig. 3) for the dynamics of a Boreal Owl (*Aegolius funereus*) population in which some proportion of the population experiences delayed reproduction. The stages in the life cycle are: Node 1—first year birds, Node 2—second-year birds that did not breed as first-year birds, and Node 3—'experienced or older' breeders. As is often the case in population models, we assume female demographic dominance (we therefore model only the female segment of the monogamous population). We parameterized the life cycle based, in part, on data collected for a Boreal Owl population in the wilderness of central Idaho (Hayward *et al.* 1993).



$F_3 = P_A * m = 0.53$
$P_3 = P_A = 0.46$
3
$G_{31} = P_1 * B_1 = 0.03$
$P_2 = P_A = 0.46$
1
2
$F_1 = P_1 * B_1 * m = 0.04$
$G_{21} = P_1 * (1 - B_1) = 0.20$
$F_2 = P_A * B_2 * m = 0.31$

Figure 3.—*A life cycle graph for a population of Boreal Owls. Node 1 represents first-year birds, Node 2 represents second-year birds that did not breed in their first year, and Node 3 represents a mixture of experienced breeder second-year birds and birds in their third year or beyond. The arcs (transitions) between Nodes 1 and 3, and between Nodes 1 and 2 are labeled* G_{ij} *because they are compound terms involving the probability of becoming a breeder at age x, denoted* B_x.

Parameterization for this stage-classified life cycle is somewhat more complicated than for a simple Leslie matrix, mostly because we are introducing a new transition parameter—the probability of becoming a breeder. Transitions therefore exist whose critical aspect is not changing age but the change from non-breeding to breeding status. We used the following estimates for the vital rates: first-year survival, $P_1 = 0.23$, 'adult' survival, $P_A = 0.46$, and $m = 1.16$ female fledglings per female. We assumed a 15 percent probability of reproduction by first-year birds (B_1), 65 percent by second-year birds, and 100 percent by all older birds. The 65 percent second-year breeding percentage points to a potential pitfall in parameterization. Remember that some (15 percent) of the first-year breeders become 'experienced' breeders and move directly to Node 3. The proportion of birds that breed in their second year but not in their first year, B_2, is therefore 0.588 ($0.15 + 0.588 * (1 - 0.15) = 0.65$ overall). Note also that Node 3 will be heterogeneous for age—a few second-year and third year birds that first bred from Node 1 or 2 (shown by reproductive arcs going back to Node 1), a few third-year first-time breeders (via the arc from Node 2 to Node 3 describing individuals that were not in the proportion B_2 that first bred in their second year) and returning experienced breeders, represented by the self-loop on Node 3.

In the life cycle we have formulated in figure 3, individuals can move to stages other than the next numerical stage. We therefore need a double subscript for transitions among stages. We specify such transitions among stages with the notation G_{ij}, where the transition is to Node i from Node j. For example, because the probability of breeding for first-year birds in Node 1, B_1, is 0.15, $G_{31} = P_1 * B_1 = 0.23 * 0.15 = 0.0345$. Note also that we must specify that individuals moving to Node 2 were yearling non-breeders by adding the term $1 - B_1$ (the probability of not breeding as yearlings). The additional 'change of status' elements, B_x and $1 - B_x$, represent the most significant difference between the formulation for an age-classified versus a stage-classified model. Other possible stage classification terms could include greater age-specificity incorporated in additional nodes, parameters describing growth (e.g., for life cycles where size is more important than age in determining survival or fertility) or nodes describing territory quality (the arcs would then describe the probability of obtaining high versus low quality territories). The possibilities are limited only by our ability to estimate important transitions in the life cycle.

ANALYSIS OF THE MODEL

The parameter estimates for vital rates (transitions) in the life cycle graph are converted to the equivalent matrix formulation (fig. 4), and then analyzed using standard matrix techniques. Although the calculations can be made rather easily employing widely available software, we emphasize the importance of correctly formulating the life cycle graph and its constituent transition values. It is difficult to obtain reliable estimates of stage specific survival and reproduction—misformulation of the life cycle graph will lead to incorrect conclusions. Time spent on carefully formulating the life cycle graph to account completely for all possible transitions is negligible compared to the field effort necessary to collect accurate data—but it is equally essential.

(a)

$$\begin{bmatrix} F_1 & F_2 & F_3 \\ P_1 & & \\ & P_2 & P_3 \end{bmatrix}$$

(b)

$$\begin{bmatrix} 0.2 & 0.6 & 1.1 \\ 0.3 & & \\ & 0.6 & 0.8 \end{bmatrix} * \begin{bmatrix} 52 \\ 16 \\ 32 \end{bmatrix} = \begin{bmatrix} 55 \\ 17 \\ 34 \end{bmatrix}$$

Figure 4.—*(a) Matrix corresponding to the life cycle graph in figure 3.*
(b) Matrix of numeric values corresponding to the graph in figure 3.

Given a correctly formulated life cycle graph and its corresponding matrix, we can assess important parameters of the population dynamics. Caswell (1989) and McDonald and Caswell (1993) describe methods to calculate the demographic metrics given in table 1. In the context of providing input for studies of habitat associations, sensitivity analysis and the measurement of individual fitness are arguably the most important metrics.

Demographic Sensitivity, Elasticity and Fitness Analysis

Demographic sensitivity means the sensitivity of λ (population growth) to changes in particular demographic rates. Sensitivity measures the impact on λ of changing the absolute magnitude of a particular vital rate (say second-year survival) relative to changing other vital rates. An extension of the sensitivity analysis is elasticity analysis, which assesses the proportional sensitivity of λ to change in a vital rate. Both sensitivity and elasticity are useful measures. One advantage of elasticities is that they are weighted by the magnitude of the original arc in the life cycle. Thus, arcs of very low magnitude tend to yield lower elasticities, even if they are quite sensitive. For example, λ might be very sensitive to a change in the probability of breeding as a yearling. If, however, that is a very rare event (say only 1 percent of owls breed as yearlings), and is unlikely to respond to changing management practices, we might be better guided by elasticities which will emphasize vital rates that are of large current magnitude and that may be more responsive to changes in management. A second advantage of elasticities is that they sum to 1.0, providing a straight forward basis for comparing elasticities across varied life histories.

Eigenvalue analysis of the projection matrix yields the elasticities and sensitivities. McDonald and Caswell (1993) provide an accessible explanation of the necessary calculations. Kroon *et al.* (1986) also discuss the uses and computation of elasticities. The computations can be performed most easily by employing software designed for matrix algebra (e.g., Mathematica, MathCad, RAMAS).

Elasticity analysis of our example life cycle for boreal owls (fig. 3) indicates that survival of breeding adults is by far the most important transition (fig. 5). Only two other transitions stand out: reproduction by adults and the transition from breeding as yearlings to becoming 'experienced' breeders. We can also calculate the mean age of the experienced and older breeders in Node 3 ($\bar{x}$ = 4.3 ± 3.0) as developed by Cochran and Ellner (1992) and other metrics outlined in table 1.

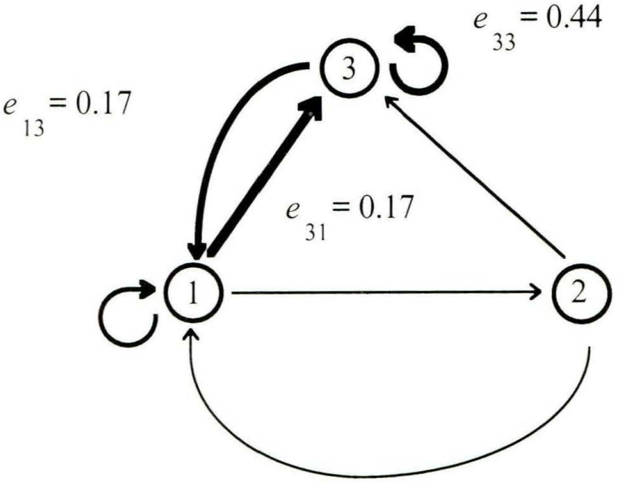


Figure 5.—*Life cycle graph corresponding to the Boreal Owl data shown in figures 3 and 4. Values represent elasticities for the three most important transitions in the life cycle.*

In a few cases, data may be sufficient to compute fitnesses directly for different habitats—possibly the ideal case for habitat analyses. McGraw and Caswell (1996) show that with data on lifetime reproduction and age at death, one can calculate an individual's 'population growth rate', λ, that serves as an integrated measure of fitness. They also show that even where data are incomplete, powerful analyses are possible. The technique is straightforward—the fitnesses are computed from the dominant eigenvalue of the reproductive outputs (half the offspring production, because our analyses are restricted to females) in the top row and survival values of 1.0 in the subdiagonal, with the dimensionality of the matrix equaling the life span of the individual. McGraw and Caswell (1996) provide examples from two long-term avian studies. By calculating a set of individual fitnesses across different habitats, one could directly assess the fitness consequences due to the habitat differences.

USING THE RESULTS FROM AN ELASTICITY ANALYSIS

Matrix models can be a powerful supplement to developing owl habitat models in at least two ways. First, it can provide the focus for gathering field demographic data. Second, it can highlight the most important life cycle transition for the species, and thereby guide the development of models customized to address the habitat variables most important to the population dynamics. We briefly discuss both of these.

Understanding the Life Cycle

A matrix model can help focus our field efforts. For example, our boreal owl model suggested that 'adult' survival was of overwhelming importance. The results suggest that field effort devoted to greater understanding of both variation in survival and the factors affecting survival would be particularly useful. Studies of clutch size, fledging success and other facets of reproduction, on the contrary, may be less worthy of intensive effort. The model can also guide the development of habitat models by ensuring that they incorporate the critical transitions in life cycle. The results of our Boreal Owl model suggests that any habitat model will need to incorporate features that affect 'adult' survival. This should, for example, emphasize studies on winter habitat and roosting site requirements.

Identifying Key Habitat

Building a sound conservation strategy for a species demands an understanding of the effect of habitat change on important demographic processes. Many studies of habitat relationships examine differences in used and available habitat, avoiding the question of how habitat characteristics are linked to demographic performance. It is not always possible to measure demographic performance in different habitats. However, when we do measure demographic performance as a metric to gage habitat quality, what metric should be used to compare the quality of habitats?

Matrix modeling provides a powerful tool to help focus habitat studies. Through elasticity analysis we can identify the demographic transitions most important in determining population growth. We can then design habitat studies that focus on the habitat elements most important to sensitive or elastic stages of the life history. We thereby provide a strong link between demography and habitat characteristics. By measuring the more 'important' vital rates in conjunction with our studies of habitat characteristics, we can rank habitats, in terms of quality, based on a defensible metric. In some cases we may even have the luxury of directly comparing individual fitness across different habitat types.

Insights from elasticity analysis can also help us identify WHAT habitat characteristics to measure. For instance, if elasticity suggests that adult survival is an important transition, and natural history observations indicate that predation is an important form of mortality for adults, our focus in habitat studies might change. Consider the potential difference in focus if we stress measures of reproduction (clutch size, fledging success) in a cavity nesting owl versus survival of adults. Management may focus on snag management in one case and characteristics related to predator risk for adults in the other. Elasticity analysis, then, may help us identify key groups of habitat variables to quantify during our studies of habitat associations. Without the insights provided by matrix analysis, we might have overlooked these habitat characteristics.

CONCLUSIONS

Matrix population models can help us; (1) determine what demographic characteristics to measure during our studies of habitat associations, and (2) focus on the habitat characteristics that have the greatest impact on population growth. Matrix models therefore represent an important tool in the design and implementation of owl habitat studies.

We caution, however, that applying matrix models to improve the design of habitat studies should not lead us to approach our work with tunnel vision. Although, matrix methods can point toward critical portions of a life cycle, we should not lose sight of the importance of other transitions. Reproduction by young birds may dominate an elasticity matrix, suggesting the importance of breeding habitat. However, this does not indicate that successful management can neglect habitat that is important for other life cycle functions. Obviously, if all the potential nest sites are gone, it doesn't matter how insensitive one was to changes in reproductive transitions. Instead, the matrix results indicate where the greatest gains may be realized in focused habitat improvement efforts.

For many biologists one of the greatest benefits of matrix modeling may come in the process of building the life cycle graph based on the life history data they have for their species. Building the graph can highlight the complexity of possible transitions and identify field data requirements.

The paucity of data on survival and reproduction may represent a barrier to application of matrix models in owl research and management. However, the ease of applying these models provides the opportunity to use them even in the face of sparse demographic data. We can learn from matrix models by exploring the behavior of the model given different assumptions regarding the vital rates of our target population. Therefore, we don't need perfect estimates of vital rates. We suggest playing WHAT-IF GAMES by observing the behavior of the elasticity matrix under a range of plausible vital rates. Frequently, analysis under assumptions that span the range of plausible values will lead to similar results, consistently identifying the same group of important transitions.

LITERATURE CITED

Alldredge, J.R.; Ratti J.T. 1986. Comparison of some statistical techniques of analysis of resource selection. Journal of Wildlife Management. 50: 157-165.

Caswell, H. 1989. Matrix population models. Sunderland, MA: Sinauer.

Cochran, M.E.; Ellner, S. 1992. Simple methods for calculating age-based life history parameters for stage-structured populations. Ecological Monographs. 62: 345-364.

Hayward, G.D.; Hayward, P.H.; Garton, E.O. 1993. Ecology of Boreal Owls in the northern Rocky Mountains, USA. Wildlife Monographs. 124: 1–59.

Kroon, H.; de, Plaisier, A.; van Groenendael, J.; Caswell, H. 1986. Elasticity: the relative contribution of demographic parameters to population growth rate. Ecology. 67:1427-1431.

Leslie, P.H. 1945. On the uses of matrices in certain population mathematics. Biometrika. 33: 183-212.

Leslie, P.H. 1948. Some further notes on the uses of matrices in population mathematics. Biometrika. 35: 213-245.

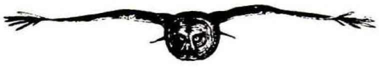
McDonald, D.B.; Fitzpatrick, J.W.; Woolfenden, G.E. 1996. Actuarial senescence and demographic heterogeneity in the Florida scrub jay. Ecology. 77: 2373-2381.

McDonald, D.B.; Caswell, H. 1993. Matrix methods for avian demography. In: Power, D.M., ed. Current Ornithology, Volume 10. New York, NY: Plenum Press: 139-184.

McGraw, J.B.; Caswell, H. 1996. Estimation of individual fitness from life-history data. American Naturalist. 147: 47-64.

Morrison, M.L.; Marcot, B.; Mannon, R.W. 1992. Wildlife-habitat relationships: concepts and applications. Madison, WI: University of Wisconsin Press. 343 p.

VanHorne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management. 47: 893-901.



Testosterone, Aggression, and Territoriality in Male Western Screech-owls (*Otus kennicottii*): Results from Preliminary Experiments

Brian L. Herting and James R. Belthoff [1]

Abstract.—Using a hormone implant protocol, we created treatment groups in which circulating levels of testosterone (T) were increased, decreased, or maintained at normal levels (controls) in male Western Screech-owls (*Otus kennicottii*). Owls were exposed to tape-recorded vocalizations of a conspecific, to which territory holders responded with aggression. Several measures of the intensity of aggression (e.g., approach and vocal behavior) provided the basis for comparisons among treatment groups. Exogenous T elicited increased aggression during the breeding and nonbreeding seasons. Although male owls remained sensitive to exogenous T during the nonbreeding season, aggression also occurred in the absence of circulating T at this time.

Aggressive defense of territories by birds during the breeding season is often associated with circulating testosterone (T) levels (Beletsky *et al.* 1990, Harding and Follet 1979, Ramenofsky 1984, Wingfield *et al.* 1987, Wingfield and Wada 1989). Elevated T allows males to compete with other males for territories and females, and to respond effectively to territorial intruders (Wingfield and Farner 1978). However, maintenance of elevated T levels is costly. For example, individuals with high T spend significantly more time in territorial defense and less time tending offspring (Hegner and Wingfield 1987, Ketterson and Nolan 1992, Silver 1977), and high T increases basal metabolism and reduces survival (Dufty 1989). Therefore, it is advantageous for birds to maintain high T only in periods when the potential for male-male interactions is greatest, such as during the breeding season, periods of territory establishment, and other periods during which instability might occur (Wingfield *et al.* 1987, 1990). Testosterone should be reduced during periods of relative social stability, i.e., late in the breeding season and during the nonbreeding season. The testes are the major source of androgens in male birds, but they regress during the nonbreeding season; consequently T levels are low at this time of the year. However, some avian species maintain and aggressively defend territories throughout the year despite the regression of testes during the nonbreeding season (Logan and Wingfield 1990). The role of T in mediating territorial defense during the nonbreeding season is less well understood (but see Logan and Wingfield 1990).

Our study was designed to understand the role of T in territorial aggression in nonmigratory species of birds that defend territories throughout the year. To understand this relationship we used the Western Screech-owl (*Otus kennicottii*) as our model species. This is an appropriate species in which to examine this relationship because:

1. male screech-owls appear to defend territories throughout the year,
2. males respond aggressively to tape-recorded conspecific vocalizations,
3. owls are easily captured using both mist nets and artificial roosting boxes which allows for radio-marking and administering of the hormone/drug treatments, and
4. a population of marked owls exists in our study area in southwestern Idaho.

We employed a hormone/drug implant protocol that experimentally increased (T_+) or decreases (T_-) testosterone in relation to control birds (T_o).

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Using approach and vocal responses to playback of tape-recorded conspecific vocalizations as indices of aggression, we examined the role of T in mediating aggression during the breeding and nonbreeding seasons.

METHODS

From January to early March, and October to December 1996, we monitored two Western Screech-owls populations in southwest Idaho. One population was located in the Snake River Birds of Prey National Conserva-tion Area (Owyhee and Elmore Counties) and the other inhabited riparian woodlands and suburban areas along the Boise River between Boise (Ada County) and Middleton (Canyon County). During both the breeding and non-breeding seasons, male owls were captured from artificial nest/roost boxes or at night using mist nets. Following capture, each individual received a subcutaneous implant containing testosterone, antiandrogenic com-pounds, or a placebo. During the breeding season, four males received exogenous T (one 20 mm implant of silastic tubing packed with crystalline testosterone, sealed at both ends); four males received the antiandrogenic drug flutamide (20 mm) and a T aromatization inhibitor, ADT (28 mm); and five males received placebo implants (20 mm). During the nonbreeding season, three males received exogenous T, two received T-inhibiting drugs, and three received placebo implants. Each male owl in both seasons were outfitted with a 5 g backpack mounted radio transmitter so that their movements could be monitored (see Belthoff and Ritchison 1989, 1990 for details on radio-transmitters and attachment). One to 2 weeks after owls received the implants, we performed the playback experiment, which consisted of three 10 minute test periods. The first period (preplayback period) involved two observers radiotracking the focal bird by taking a compass bearing of its position each minute during the experiment. The second 10 minutes, the playback period, was similar to the first, except that during this period we broadcast taped-recorded vocalizations of a conspecific (i.e., simulated territorial intruder; one of three different tapes was played during each experiment) from a speaker placed within the territory (100 m from the nest or focal roosting area) of each radio-tagged focal owl. Again, compass bearings of the owl's location were recorded every minute. The third 10 minutes, the postplayback period, was identical to the preplayback period. Compass bearings were later plotted to determine the owl's distance from the speaker during each minute of the 30 minute playback experiment. During each playback experiment we determined distance (m) of the focal owl from the playback speaker during each minute, the overall closest approach (m) to the playback speaker by the focal owl during any of the three test periods (in all cases this occurred during the playback period), the number of vocalizations uttered by the focal owl during each of the test periods (any vocal responses by the focal owls were tape-recorded during the experiment using a directional microphone and later counted), and the number of minutes that the focal owl continued to call into the 10 minute postplayback period (maximum of 10 minutes/ referred to as duration of calling). We assumed that owls that called more and approached the playback speaker more closely were the most aggressive.

To control for variation in T related to breeding stage, all experiments during the breeding season were performed while the focal owl's mate was incubating eggs, a time period during which circulating levels of T are typically high (B. Herting, J. Belthoff, and A. Dufty, unpubl. data). During the nonbreeding season, all experiments were performed during November and December, a time period when T levels are very low (B. Herting, J. Belthoff, and A. Dufty, unpubl. data). All data were analyzed using single way or multiway analysis of variance (ANOVA), and repeated measures analyses were conducted where appropriate. To examine effects of treatment, season, and period on distance, the 10 locations of each focal owl (obtained from compass bearings) were averaged for each period of the playback experiment, and these averages were entered into the analysis. Post hoc means comparisons were performed using pairwise t-tests.

RESULTS AND DISCUSSION

Effects of Playback Protocol on Aggression by Focal Males

Our first objective was to determine whether the tape-recorded vocalizations elicited an aggressive response by focal owls. We compared two indices of aggression, vocalizations and distance from speaker, among test periods. When the playback stimulus was applied, we expected resident males to approach the

Table 1.—*Mean (± SE) distance from the playback stimulus and mean (± SE) number of vocalizations uttered by each focal male Western Screech-owl during the three playback periods (see text for description of playback periods) during 21 playback experiments in southwestern Idaho during 1996. Values are averaged across seasons and treatment groups.*

Variable	Playback period			Period effect
	Preplayback	**Playback**	**Postplayback**	
Distance from playback speaker (m)[1]	96.0 ± 13.9	64.7 ± 13.9	63.7 ± 13.9	$F_{2,30} = 1.73$ $P = 0.19$
Number of vocalizations uttered	1.7 ± 3.4	25.7 ± 3.4	13.7 ± 3.4	$F_{2,30} = 12.24$ $P = 0.0001$

[1] Average of 10 locations obtained during each playback period for each focal owl were entered into analysis for this variable.

speaker and call in response to the simulated territorial intrusion by another male screech-owl. In line with this expectation, focal owls vocalized significantly more often during the playback and postplayback periods than during the preplayback period (table 1). Moreover, the average distance between the focal owl and the playback speaker was lower during the playback and postplayback periods (table 1), although differences among test periods were not significant ($P = 0.19$). The lack of significance associated with the lower average distance during the playback period may have resulted from large variation in the focal owl's initial distance from the playback speaker during the preplayback period. For example, at the beginning of the experiment some owls were very close to the playback speaker and moved relatively closer, while other owls were initially very far away and approached when the playback began. There was no significant effect of season (breeding vs. nonbreeding) on average distance from playback speaker ($F_{1,15} = 1.89$, $P = 0.189$) or total vocalizations uttered during the 30 minute experiment ($F_{1,15} = 1.90$, $P = 0.187$). These latter results indicate that the aggressive response of focal males toward the playback stimulus was similar between seasons, and they are consistent with the hypothesis that these screech-owls are territorial throughout the year.

Effects of Hormone/Drug Treatments on Aggression by Focal Males

Approach Behavior Toward Playback Stimulus

There was a significant effect of treatment on average distance from the playback stimulus (table 2); owls treated with exogenous T were significantly closer to the playback speaker than owls whose T production and uptake were blocked. This result suggests that the drug/hormone implants were efficacious, that birds treated with exogenous T were significantly more aggressive, and that owls treated with T-blocking drugs showed decreased aggression. In addition, owls treated with T during the nonbreeding season exhibited aggressive responses comparable to owls that received exogenous T during the breeding season (table 2). This result indicates that, even though circulating T levels are normally very low during the nonbreeding season, male Western Screech-owls continued to be sensitive to the presence of this steroid hormone throughout the year. Finally, owls treated with T approached the speaker most closely (e.g., closest approach to the playback speaker during the entire 30 minute experiment) when compared to owls in either of the other two treatment groups, although the difference among groups was significant only at the $P = 0.10$ level (table 2).

Table 2.—*Aggression indices (mean ± SE) by season for each treatment group of Western Screech-owls in southwestern Idaho. Numbers in brackets represent sample sizes.* T_+ *refers to subjects whose testosterone levels were experimentally increased,* T_- *individuals had testosterone levels lowered experimentally, and testosterone levels in* T_0 *were allowed to fluctuate naturally. There were no significant season effects (P values for seasons ranged from 0.08 to 0.18 for each variable below) or interactions with treatment, F- and P-values are shown for treatment effects only.*

	T_+		T_-		T_0		
Aggression indices	**Breeding {4}**	**Nonbreeding {3}**	**Breeding {4}**	**Nonbreeding {2}**	**Breeding {5}**	**Nonbreeding {3}**	**Treatment effect**
Mean distance from speaker (m)[1]	28.7 ± 30.6	17.6 ± 35.4	162.1 ± 30.6	96.2 ± 43.3	41.1 ± 27.4	42.5 ± 35.4	$F_{2,15} = 3.95$ P = 0.04
Overall closest approach to speaker (m)	4.9 ± 5.4	5.4 ± 6.3	8.7 ± 5.4	27.0 ± 7.7	13.0 ± 4.8	18.6 ± 6.3	$F_{2,15} = 2.57$ P = 0.10
Total number of vocalizations	72.0 ± 16.6	84.0 ± 19.2	50.5 ± 16.6	0.0 ± 23.5	49.8 ± 14.9	4.0 ± 19.2	$F_{2,15} = 5.43$ P = 0.02
Duration of vocalization (min.)	8.5 ± 1.6	9.3 ± 1.8	3.3 ± 1.6	0.0 ± 2.2	5.0 ± 1.4	0.0 ± 1.8	$F_{2,15} = 10.4$ P = 0.001

[1] Average of 10 locations during each playback period for each focal owl were entered into analysis for this variable.

Vocal Response to Playback Stimulus

Owls treated with T uttered significantly more vocalizations and continued to vocalize longer into the postplayback period following removal of the playback stimulus (table 2) than owls in the other two groups. We detected no differences in the total number or duration of vocalizations between T-blocked and control birds, particularly during the nonbreeding season. This suggests that although exogenous T increases calling during both seasons, owls treated with T-blocking drugs are just as likely as control owls to vocalize in response to the playback stimulus.

CONCLUSIONS

Our results suggest that Western Screech-owls express aggressive behavior during both the breeding and nonbreeding seasons, which is consistent with the observations that these owls are territorial throughout the year. Our study also suggests that T is an important mediator of aggression in male screech-owls during the breeding season; owls with high T were most aggressive and when T was blocked aggression was reduced. Although they remained sensitive to T during the nonbreeding season (a time period when circulating T levels are normally low), male Western Screech-owls exhibited aggressive behavior comparable to that observed during the breeding season. This suggests that some other neuroendocrine mechanism may regulate aggression in these owls during this time. Our goal is to perform additional playback experiments during both the breeding and nonbreeding seasons in 1997 to clarify the relationships among testosterone, territoriality, and aggression in male Western Screech-owls.

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LITERATURE CITED

Beletsky, L.D.; Orians G.H.; Wingfield J.C. 1990. Effects of exogenous androgen and antiandrogen on territorial and nonterritorial Red-winged Blackbirds (Aves: Icterinae). Ethology. 85: 58-72.

Belthoff, J.R.; Ritchison, G. 1989. Natal dispersal of Eastern Screech-owls. Condor. 91: 254-265.

Belthoff, J.R.; Ritchison, G. 1990. Roosting behavior of postfledging Eastern Screech-owls. Auk. 107: 567-579.

Dufty, A.M., Jr. 1989. Testosterone and survival: a cost of aggressiveness? Hormones and Behavior. 23: 185-193.

Harding, C.H.; Follet, B.K. 1979. Hormone changes triggered by aggression in a natural population of blackbirds. Science. 203: 918-920.

Hegner, R.E.; Wingfield, J.C. 1987. Effects of brood-size manipulations on parental investment, breeding success, and reproductive endocrinology of House Sparrows. Auk. 104: 470-480.

Ketterson, E.D.; Nolan, V., Jr. 1992. Hormones and life histories: an integrative approach. American Naturalist. 140: S33-S62.

Logan, C.A.; Wingfield, J.C. 1990. Autumnal territorial aggression is independent of plasma testosterone in mockingbirds. Hormones and Behavior. 24: 568-581.

Ramenofsky, M. 1984. Agonistic behavior and endogenous plasma hormones in male Japanese quail. Animal Behaviour. 32: 698-708.

Silver, R. 1977. Effects of the antiandrogen cyproterone acetate on reproduction in male and female ring doves. Hormones and Behavior. 9: 371-379.

Wingfield, J.C.; Farner, D.S. 1978. The annual cycle in plasma irLH and steroid hormones in feral populations of the White-crowned Sparrow, *Zonotrichia leucophrys gambelii.* Biological Reproduction. 19: 1046-1056.

Wingfield, J.C.; Wada, M. 1989. Changes in plasma levels of testosterone during male-male interactions in the Song Sparrow, *Melospiza melodia*: time course and specificity of response. Journal of Comparative Physiology. 166: 189-194.

Wingfield, J.C.; Hegner, R.E.; Dufty, A.M., Jr.; Ball, G.F. 1990. The 'challenge hypothesis': theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. American Naturalist. 136: 829-846.

Wingfield, J.C.; Ball, G.F.; Dufty, A.M., Jr.; Hegner, R.E.; Ramenofsky, M. 1987. Testosterone and aggression in birds. American Scientist. 75: 602-608.

A Sensitivity Analysis of a Map of Habitat Quality for the California Spotted Owl (*Strix occidentalis occidentalis*) in Southern California

Ellen M. Hines and Janet Franklin[1]

Abstract.—Using a Geographic Information System (GIS), a sensitivity analysis was performed on estimated mapping errors in vegetation type, forest canopy cover percentage, and tree crown size to determine the possible effects error in these data might have on delineating suitable habitat for the California Spotted Owl (*Strix occidentalis occidentalis*) in southern California. The maps were developed as part of a project to map existing vegetation for the USDA Forest Service in southern California using Landsat Thematic Mapper satellite data, and GIS modeling. The research area is the San Bernardino National Forest, the largest contiguous area of spotted owl habitat in southern California, with a large and thoroughly surveyed spotted owl population. Map error was estimated using error matrices based on comparing the final map output to expert photointerpretation of a number of locations. The simulation of map uncertainty resulted in an increase in suitable habitat area with changes in vegetation classification. There was no significant increase in the number of actual known spotted owl locations found with modeled areas of suitable habitat. Fragmentation analysis of the additional patches showed a possibility that the additional patches were too small and fragmented to be useful as actual habitat areas. This research will generate different map realizations for a population model being developed for the USDA Forest Service.

The population of the California Spotted Owl (*Strix occidentalis occidentalis*) in southern California is declining and the cause is not known (Anderson and Mahato 1995, LaHaye *et al.* 1994, Verner *et al.* 1992). Even if this decline is temporary, Lehaye *et al.* (1994) believe that the southern California metapopulation could be extinct within 40 years. Both the Northern and Mexican Spotted Owls (*S. o. caurina* and *S. o. lucida*) have been given the status of threatened by the U.S. Fish and Wildlife Service because of population decline due to loss of habitat (LaHaye *et al.* 1994, Verner *et al.* 1992). However, the California owl, which inhabits the Sierra Nevada and the Peninsular ranges of southern California, is listed as sensitive under the Endangered Species Act (LaHaye *et al.* 1994), and as a species of Special Concern by the State of California (Gutierrez *et al.* 1995). While not protected by law in the same manner as a threatened or endangered species (Greif 1995), this classification still describes the danger of a population in severe enough decline that extinction is a possibility if current management trends continue (Roberts 1993).

Although the California Spotted Owl does not require as large a territory as the Northern Spotted Owl, the amount of range the owl does require in southern California is in conflict with urban and residential expansion (Verner and Taylor 1992).

In the Hearing of the Subcommittee on National Parks, Forests, and Lands of the 104th Congress, the fact that the California Spotted Owl was classified as sensitive rather than endangered led politicians to argue that the management of this species was expensive, unnecessary, and politically dangerous (California Spotted Owl Recovery Plan Hearing 1994). The vigorous debate which seemingly pits politicians and economists against ecologists and academics could be seen as a test of the values which have guided our resource management agencies in recent years (Gutierrez *et al.* 1995, Yaffee 1994). The intensity of political debate has overshadowed the fact that much still needs to be learned about the life history and ecology of the owl in order to develop a plan for the conservation of this species (Gutierrez *et al.* 1995, Verner *et al.* 1992). Explicit characterizations of habitat requirements for the California Spotted Owl still must be assumed. These assumptions could make the conclusions of habitat models cur-rently being developed highly suspect, and possibly too general for the critical habitat designation of a sensitive or possibly threatened species (Heinen and Lyon 1989, Verner and Taylor 1992). Isolating the variables, whether based on owl life history, environmental factors, or human interference, which are critical to the California Spotted Owl, is now essential for the owl's survival. Population simulation models, designed to investigate the influence of these variables, have been used to examine the viability of Spotted Owl populations (Doak 1989, Lande 1988, Schumaker, in press).

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The focus of our research is aimed at one of the pitfalls of computer simulation modeling, especially the modeling of habitat in large ecosystems. Simulation approach models are "...only as good as the data on which they are based" (Moffat 1994). Problems of data availability can be avoided in these population models, provided there is a thorough analysis of the sensitivity of the results to changes in model parameters (Durant and Mace 1994). This can also be true for the error inherent in data analysis and classification based on combining Geographic Information Systems (GIS) and remote sensing mapping procedures. When using these procedures to model habitat suitability, the errors created by mapping processes, especially data classification, can effect the model critically, and some measure of this uncertainty should be known (Goodchild 1994). We attempted to characterize this uncertainty by ascertaining how sensitive habitat suitability predictions might be to reasonable assumptions of mapping process error. This knowledge can be used to more accurately isolate the importance of population model parameters. John Stephenson (pers. comm.) suggested three map classification criteria that are supposed to be the most important in the delineation of California Spotted Owl habitat: vegetation type, forest canopy cover percentage, and tree crown size. We chose an area in southern California (the San Bernardino Mountains) with a large, well-documented population of owls (LaHaye and Gutierrez 1994, Stephenson 1991). Estimating reasonable error in the mapping procedures, we then performed a sensitivity analysis to ascertain the resulting differences in delineation of habitat suitability areas using a GIS map overlaying procedure. Differences were evaluated based on comparisons with known owl locations and by other criteria. In this way, the susceptibility of the habitat suitability map to data error was quantified, and different realizations of the habitat areas with corrections based on estimated map inaccuracies were made available for the population modeling process being done for the owl by the USDA Forest Service.

The Nature of Wildlife Habitats and Habitat Models

There has been an increase in wildlife habitat modeling recently, but it has been noted that empirical testing of these models has been neglected (Chalk 1986, Stoms *et al.* 1992). Predictive wildlife habitat models, often created deductively by using expert opinions of relationships and variables, can potentially lead to erroneous conclusions. When the model wrongly predicts species presence, and the species is absent, this is a Type I error. If the model is used to purchase, or set aside land for habitat, this could be costly. When the model wrongly predicts absence, and the species is present, or a Type II error, this can be more critical, for example, when the model is being used to predict impacts on habitats for endangered or threatened species (Morrison *et al.* 1992).

In summary, wildlife habitat models examine a complex system. An attempt must be made to identify all the important components of this system with as much accuracy as possible and relate them to one another. They must be well understood and evaluated for accurate prediction of future events (Anderson and Gutzwiller 1994).

Evaluating the Sensitivity of Habitat Suitability Models

In complex decision-making, sensitivity analysis for modeling land use suitability is originally an urban planning concept, an experiment that involves a systematic manipulation of variables or factors within a study to see how other variables are affected. This can ensure that criteria are relevant and reduce uncertainty, testing the robustness, or imperviousness to perturbation of the decision model (Alexander 1989).

Lodwick *et al.* (1990) describe a sensitivity analysis using a GIS. The analysis is defined as "...the study of the effects of imposed perturbations (variations) on the inputs of a geographical analysis on the outputs of that analysis." The ability of a GIS to perform a task "...repetitively with unchanging precision makes it an effective tool for this type of modeling" (Lowry *et al.* 1995).

Stoms *et al.* (1992) estimated the sensitivity of habitat models to uncertainty in input data for the endangered California Condor (*Gymnogyps californianus*). He concluded, that for GIS, there is a need to acknowledge and quantify uncertainties and "...increase our confidence that GIS-based analysis provides us with a reasonable model...of (wildlife) habitat."

Habitat Fragmentation

Error in mapped habitat variables not only affect their total estimated area, but the estimated spatial arrangement of habitat patches as well. The size, shape, spatial distribution, and density of patches create the degree of habitat fragmentation within a landscape (Ripple *et al.* 1991). Habitat fragmentation was used in this research as a tool to analyze the effects of the sensitivity analysis model on output habitat patches. Fragmentation can be defined by its actions, a reduction in habitat area, and an increase in the isolation of habitat patches (Morrison *et al.* 1992, Wilcove 1985).

Fragmentation can lead to the isolation of a population causing increased risk from natural catastrophes, genetic inbreeding depression, or demographic variability. It has been shown that for species associated with forest interiors, especially populations associated with a specialized forest stand type, such as the Spotted Owl, the degree of fragmentation will cause a corresponding decline in population (Hunter *et al.* 1995, Morrison *et al.* 1992, Usher 1987). The idea of fragmentation also addresses such issues as the effects of habitat patch size and connectivity on Spotted Owl population stability. Gutierrez and Pritchard (1990) predict that the ability of juvenile owls to find vacant habitat will be critical to the health of populations in managed forests.

THE CALIFORNIA SPOTTED OWL

Geographic Range of the Spotted Owl in Southern California

The entire range of the California Spotted Owl is from the southern Cascades through the Sierra Nevadas, throughout the mountain ranges of southern California, and into the central Coast Ranges into Monterey county (Beck and Gould 1992). Gutierrez *et al.* (1995) extend the range south to Sierra San Pedro Martir in northern Baja California. In southern California, the Spotted Owl is found on 11 major mountain ranges (fig. 1). The majority of Spotted Owl populations in southern California are on National Forest lands, including the Angeles, San Bernardino, Cleveland, and Los Padres National Forests (Beck and Gould 1992).

Patterns of Habitat Use

California Spotted Owls occur in three distinct forest types in southern California. The distribution of these types is generally divided by elevation, with a riparian hardwood habitat below 1,200 m, Douglas-fir (*Pseudotsuga menziesii*)/live oak woodland (*Quercus ssp.*) forest between 900 and 1,800 m, and mixed conifer between 1,500 and 2,400 m. Forty-one percent of the owl sites in southern California occur in the big-cone Douglas-fir/live oak woodland community. The patches of forest they inhabit are dense and mature, requiring between 200 and 1,000 ha of forest per pair of birds (Verner *et al.* 1992).

California Spotted Owls are intolerant of high temperatures, seeking cool, shaded, thick (greater than 70 percent canopy cover) nesting sites. They avoid grasslands, chaparral, and open-canopied habitats (Gutierrez and Pritchard 1990, Verner *et al.* 1992). Nesting trees are usually large, with a diameter at breast height

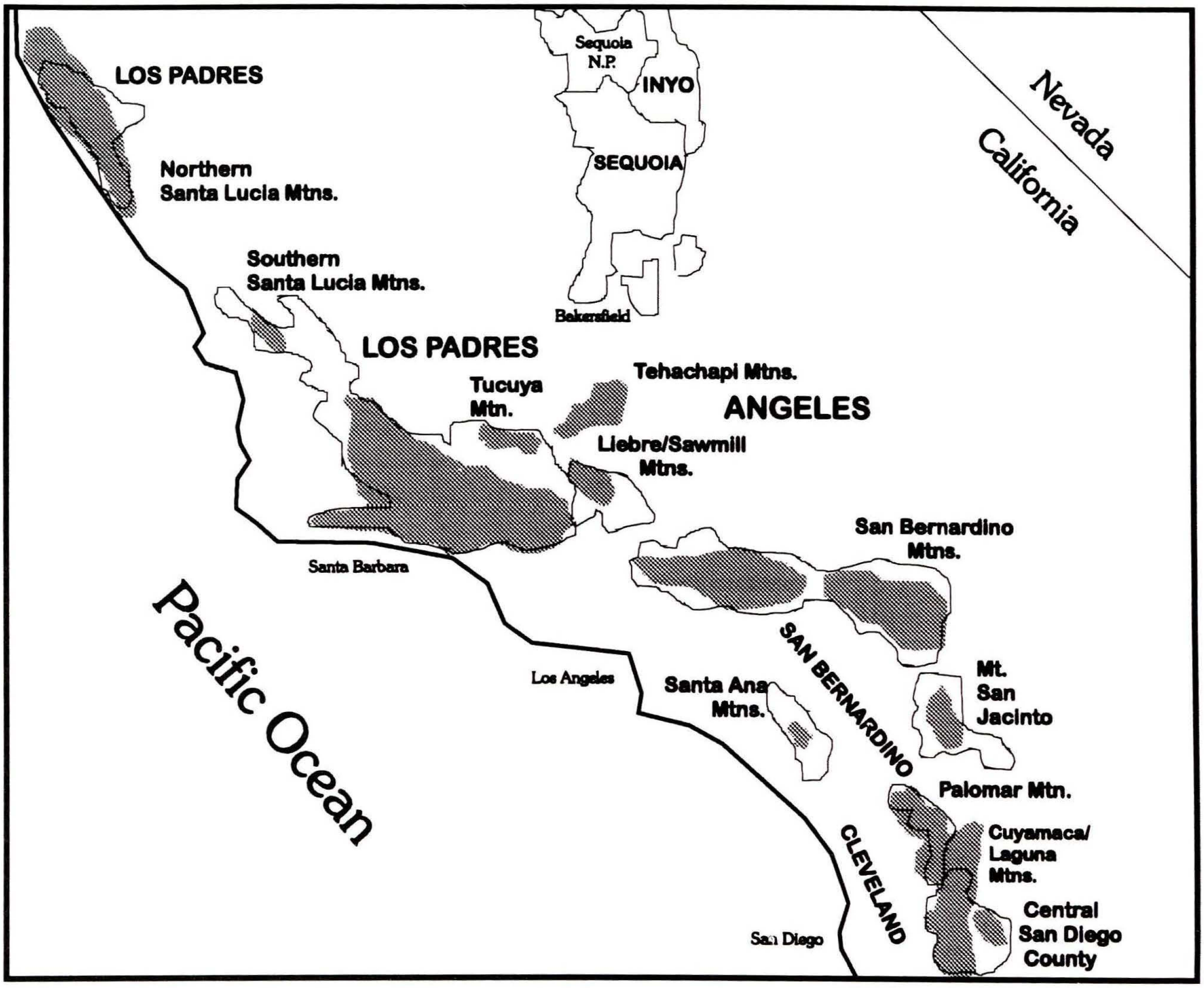
LOS PADRES
Northern Santa Lucia Mtns.
Southern Santa Lucia Mtns.
Sequoia N.P.
INYO
SEQUOIA
Bakersfield
Nevada
California
LOS PADRES
Tucuya Mtn.
Tehachapi Mtns.
ANGELES
Liebre/Sawmill Mtns.
Santa Barbara
San Bernardino Mtns.
Pacific Ocean
SAN BERNARDINO
Los Angeles
Santa Ana Mtns.
Mt. San Jacinto
Palomar Mtn.
Cuyamaca/ Laguna Mtns.
CLEVELAND
San Diego
Central San Diego County

Figure 1.—*Shaded areas show islands of population for the southern California Spotted Owl in Cailifornia. Source: Verner* et al. *(1992).*

of around 94 cm. Foraging areas are similar, but usually have lower canopy cover, usually 40 to 70 percent. The forest structure is usually complex, with trees in different diameter classes, but with a uniform presence of large trees greater than 90 cm diameter at breast height (Verner *et al.* 1992).

There are gaps between the isolated mountain ranges that constitute owl habitat in southern California that may restrict movement. The separation of suitable habitat by areas of urban development, major highways, and hot, dry lowlands is a major problem for owl dispersal. A primary concern is that this isolation will worsen. Major threats to southern California habitats include increased areas of urbanization and recreation, wildfires, and groundwater extraction. There are considerable private land holdings within National Forest boundaries which include heavily trafficked, rapidly developing recreational areas (Beck and Gould 1992). For example, in the San Bernardino National Forest, if these present trends continue, including the rapid growth of mountain resorts like Lake Arrowhead, the owl population is expected to decline by 50 percent in 4 years (LaHaye and Gutierrez 1994, Noon and McKelvey 1992, Stephenson 1991). It is becoming clear that the most important habitat variable for spotted owls in southern California is the distribution and shape of contiguous areas of suitable habitat (Gutierrez and Pritchard 1990, Lamberson *et al.* 1994).

METHODS

Description of the Study Area and Owl Sighting Data

The area used for this study is the San Bernardino Mountains, which are contained within the San Bernardino National Forest (fig. 2). Seventy km (43 miles) east of Los Angeles, these mountains are the largest contiguous area of suitable California Spotted Owl habitat in southern California (LaHaye and Gutierrez 1994). The Spotted Owl population here is also the largest in the southern California region, and the most thoroughly surveyed (Stephenson 1991). Since 1987, LaHaye and Gutierrez have made yearly population surveys. This area (1,890 km^2) is bounded on the north, east, and south by the National Forest boundary, and on the west by Interstate Highway 15 (LaHaye and Gutierrez 1994). This population is large enough (145 known territories) for demographic studies, but at the same time, small enough to monitor.

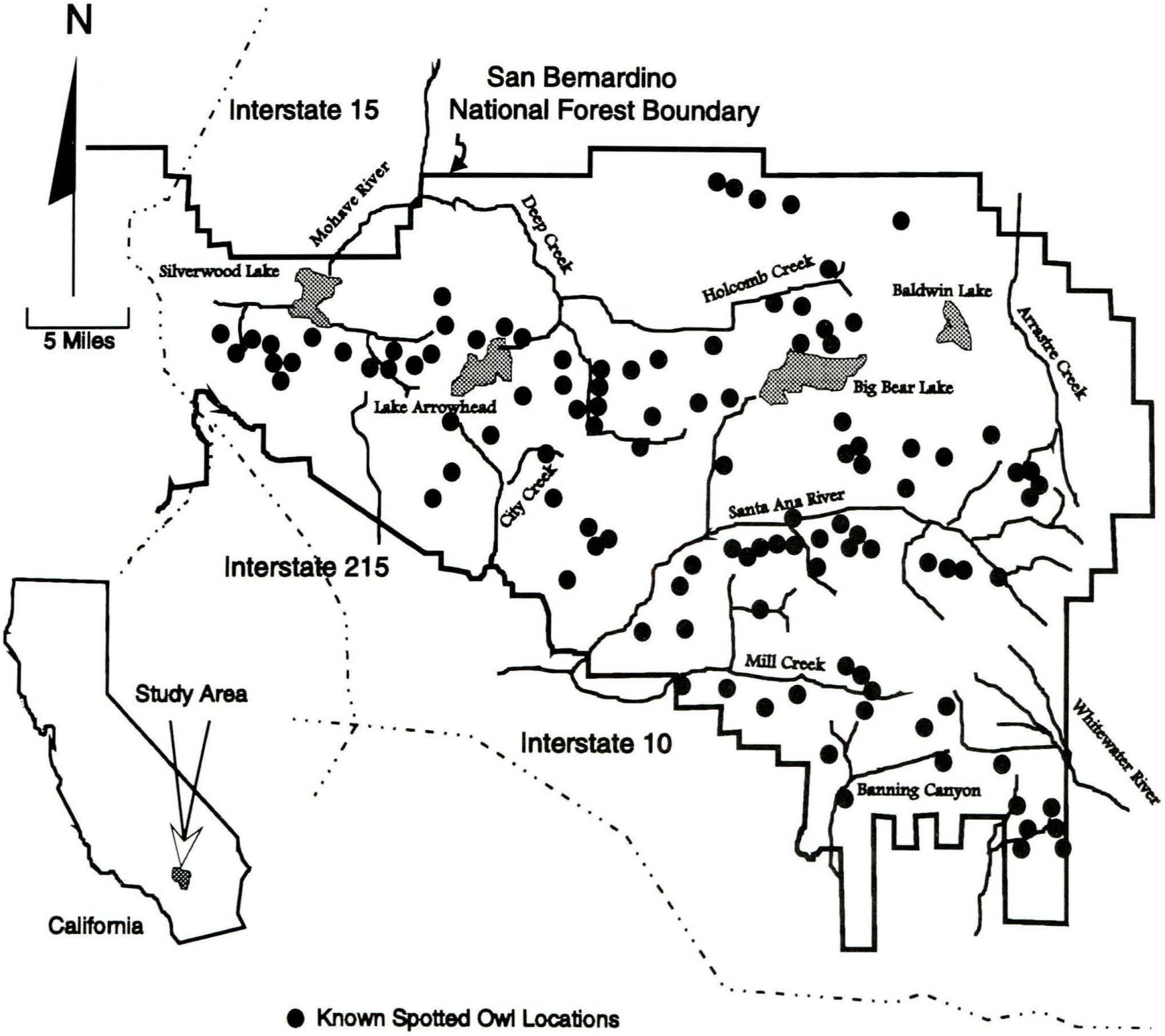
N
5 Miles
Interstate 15
San Bernardino
National Forest Boundary
Mohave River
Deep Creek
Silverwood Lake
Holcomb Creek
Baldwin Lake
Arrastre Creek
Lake Arrowhead
Big Bear Lake
City Creek
Santa Ana River
Interstate 215
Mill Creek
Study Area
Interstate 10
Whitewater River
Banning Canyon
California
● Known Spotted Owl Locations

Figure 2.—*The San Bernardino mountains Spotted Owl study area, southern California. Source: LaHaye and Gutierrez (1994).*

This research uses 629 known owl sightings documented by LaHaye and Gutierrez (1994). The locations of each sighting were recorded in UTM coordinates, and digitized into an Arc/Info point coverage. This point coverage was then converted into a Grid raster coverage with 25 x 25 m pixels for analysis. Due to overlapping locations within pixels, there are 428 pixels in the Grid raster coverage that contain owl locations.

Description of Vegetation Data

The data used in this study to represent mapped habitat variables are the result of a project utilizing remotely sensed data and GIS-modeling to map existing vegetation in the National Forests of Southern California for the USDA Forest Service. These maps provide a digital database of existing vegetation and forest cover and structure for land cover inventory, ecosystem management planning, and timber inventory of National Forest lands (Franklin and Stephenson 1996, Franklin and Woodcock 1997). The software used included Image Processing Workbench, and ARC/INFO Grid as a GIS. The Calveg vegetation classification system was used. This is a standard statewide vegetation classification system developed by the USDA Forest Service (Forest Service, Region 5, 1994). The attributes of these vegetation maps included vegetation classes, as well as estimates of canopy cover and tree crown size, and they were in a GIS database.

Accuracy Analysis of Map Data

The reference data used to estimate the accuracy of vegetation classification, canopy cover percentage, and crown size class were gathered as training sites by Harry L. Bowlin, a professional forester and consultant for the mapping project. He photointerpreted stands of designated vegetation classes, and estimated canopy percentage and crown size class for each stand. We created error matrices (Jensen 1996) by comparing the vegetation class and attributes of each stand (126 conifer stands, 97 hardwood stands) to the classes and values for the same stands in the digital maps. Based on the resulting error matrices, estimates were then made of the approximate error in the map labels.

Description of Sensitivity Analysis

The maps used in the sensitivity analysis were derived from the final map products delivered to the Forest Service (figs. 3, 4, and 5). These were produced in ARC/INFO Grid format with 25 m pixels, and a subarea was selected to represent the major owl habitat area.

To implement the changes in the maps which would represent the estimated mapping errors in vegetation class, canopy cover, and crown size found in the error matrix, programs were written in Arc Macro Language (AML) to mask ARC/INFO Grid pixels into the original polygons, and then randomly choose a specified percentage of pixels from the segments of each class, and change them into another class.

The percentages of pixels to be reassigned among the different classes were derived from the error matrices and inserted into the AML programs, which were then used to assign randomly located changes in class labels in a series of 10 replications each for the vegetation, canopy cover, and crown size maps of the area. Then the resulting maps were combined into six combinations of map change scenarios for a total of 60 iterations. The map classes were given scores of habitat value (1 through 99) using a score assessment developed by John Stephenson (pers. comm.). We then chose, in consultation with Stephenson, a threshold value of 27 to distinguish between suitable and unsuitable habitat. The area of vegetation types important as spotted owl habitat (Douglas-fir, mixed conifer, black oak (*Quercus kelloggii*), and live oak (*Quercus* ssp.) woodland) were compared with the original forest map. Also areas of canopy cover and crown size classes were compared with values in the unchanged map. The ability of these simulated corrections to significantly alter the resulting habitat suitability map was analyzed. A Wilcoxon signed rank non-parametric test was used for all significance tests, and the null hypothesis of no difference was rejected when $p < 0.05$.

Binary maps were then created from the 60 altered maps and the original unchanged map of either acceptable (1) or unacceptable (no data) areas for owl habitat based on a threshold value of 27 for suitable habitat. The area of

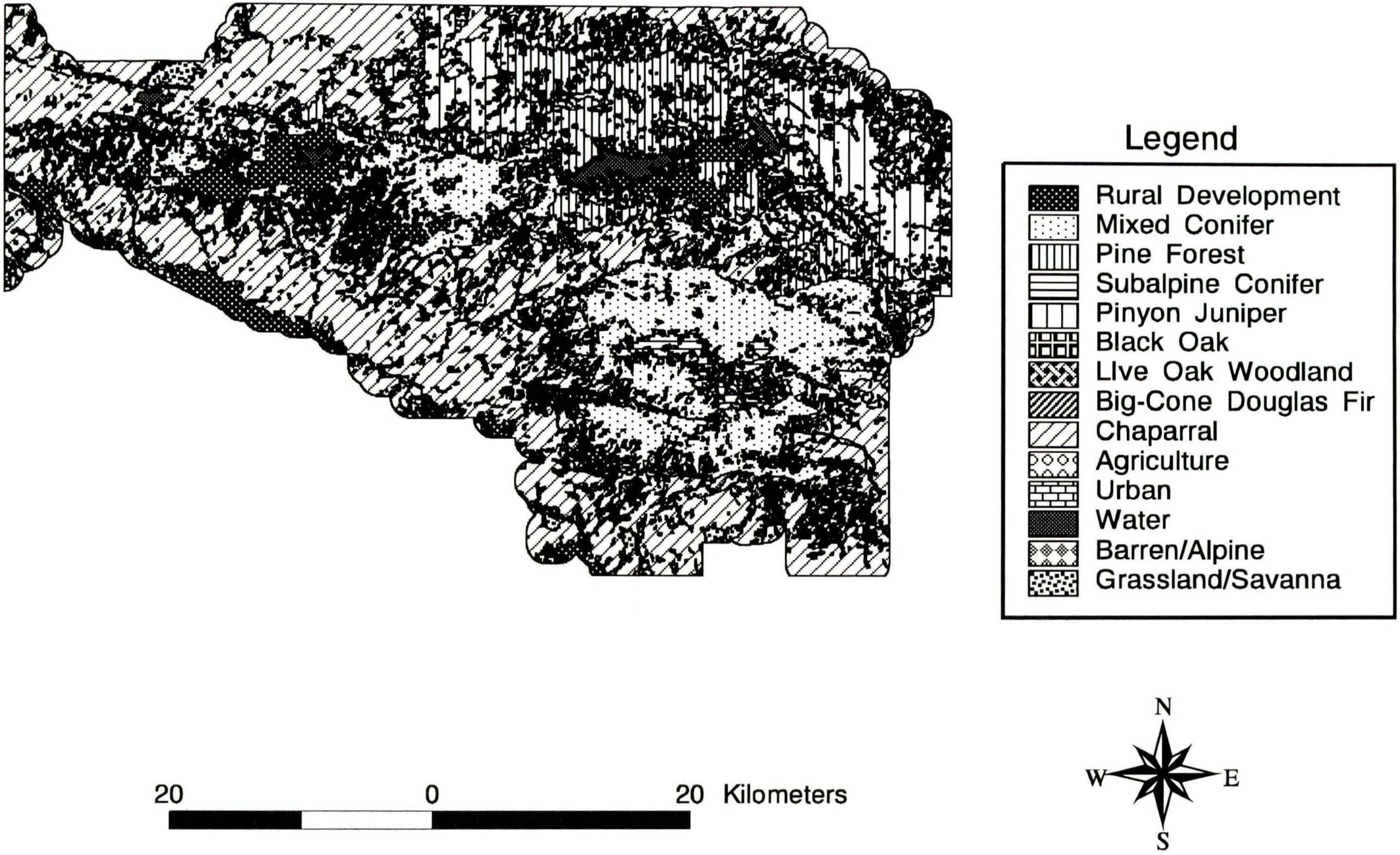
Legend
Rural Development
Mixed Conifer
Pine Forest
Subalpine Conifer
Pinyon Juniper
Black Oak
LIve Oak Woodland
Big-Cone Douglas Fir
Chaparral
Agriculture
Urban
Water
Barren/Alpine
Grassland/Savanna
20
0
20 Kilometers
N
W
E
S

Figure 3.—*Vegetation map of the San Bernardino National Forest, California, including 1.6-km (1-mile) buffer around the forest boundary. Source: U.S. Forest Service, Region 5.*

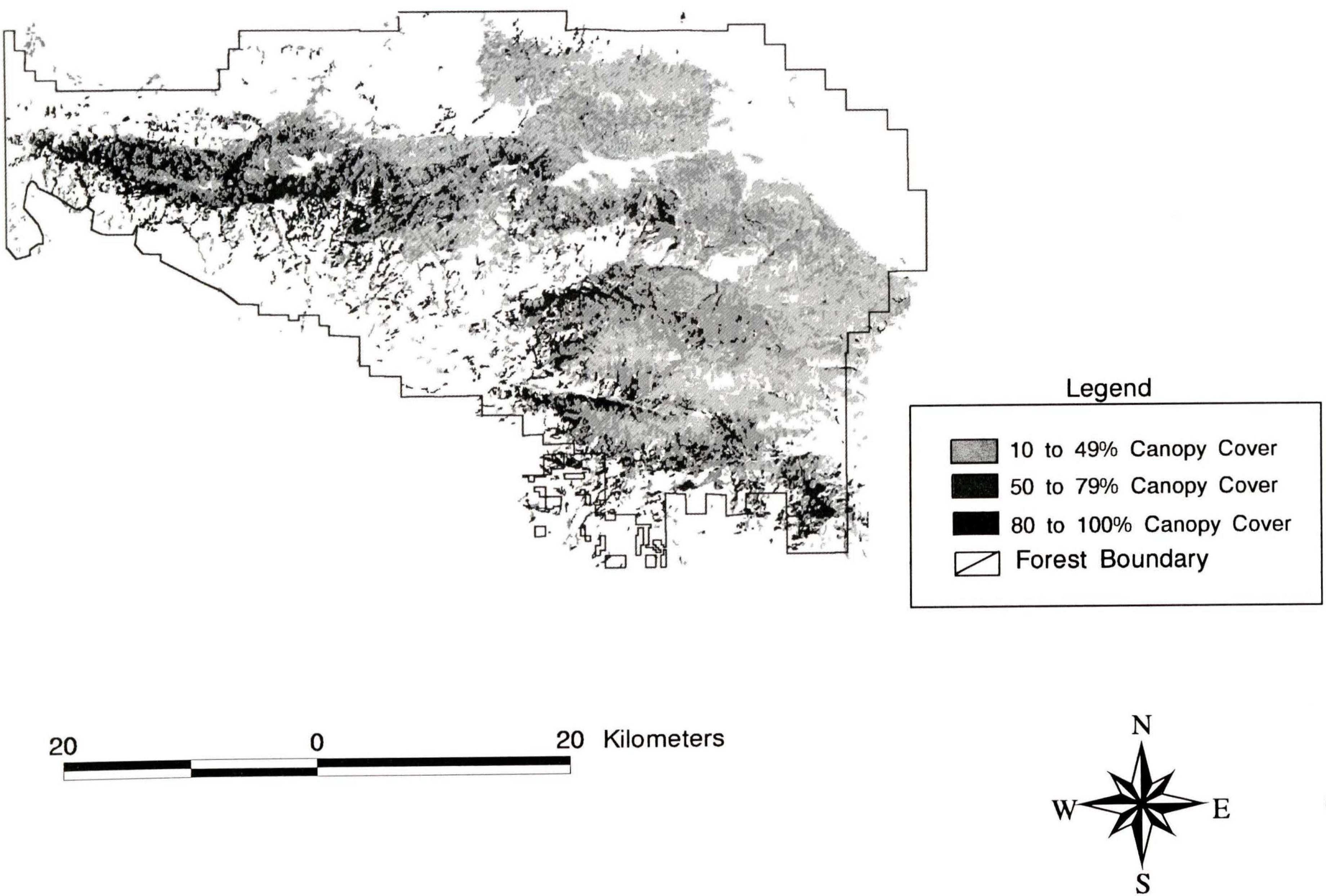
Legend
▨ 10 to 49% Canopy Cover
▨ 50 to 79% Canopy Cover
■ 80 to 100% Canopy Cover
▨ Forest Boundary
20
0
20 Kilometers
N
W
E
S

Figure 4.—*Canopy cover class map of the san Bernardino National Forest, California. Source: U.S. Forest Service.*

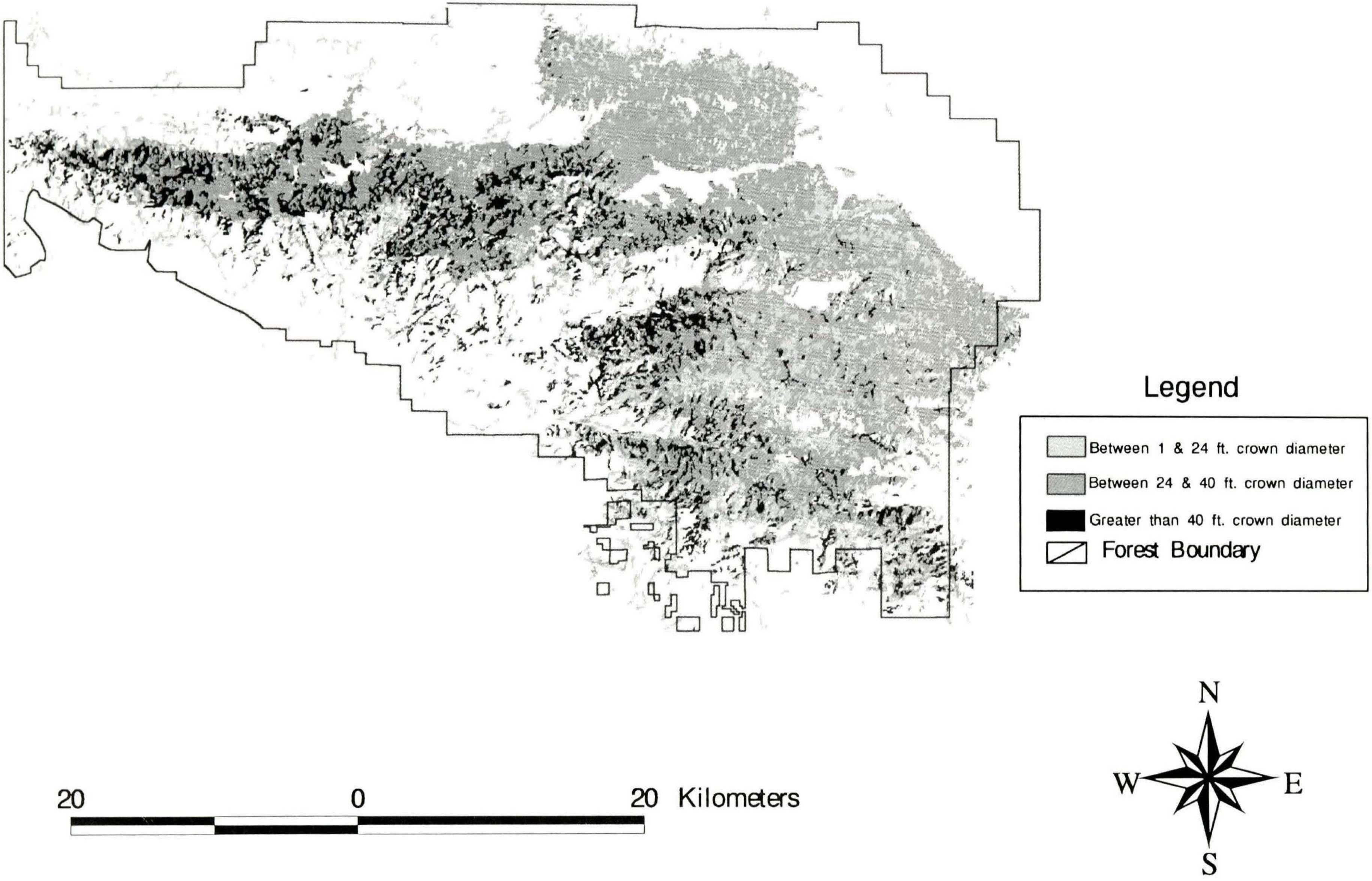
Legend
Between 1 & 24 ft. crown diameter
Between 24 & 40 ft. crown diameter
Greater than 40 ft. crown diameter
Forest Boundary
20
0
20 Kilometers
N
W
E
S

Figure 5.—*Crown size map of the San Bernardino National Forest, California. Source: U.S. Forest Service.*

acceptable habitat in each of the 60 binary maps was compared with the original map. We then compared the difference in the ability of the original habitat suitability map and those with simulated corrections to capture the actual documented owl sighting locations.

Analysis of the Effects of Simulated Map Error on Landscape Patterns of Habitat

The landscape pattern analysis software FRAGSTATS was used to evaluate the effect of simulated map corrections on spatial patterns in the predicted owl habitat (McGarigal and Marks 1994). The 60 binary maps of habitat/non-habitat were evaluated using seven landscape indices chosen to best represent the changes in the spatial pattern of the habitat and the landscape. More detailed explanations of those specific indices can be found in McGarigal and Marks (1994), and Ripple *et al.* (1991). As in Ripple *et al.* (1991), the measures chosen were related to the size, shape, distribution, and density of habitat patches. For each index, the mean values for each combination of changed maps were then compared to the values for the original map.

RESULTS

Estimating Map Uncertainty and Creation of the Sensitivity Model

Table 1 shows a sample of the error matrices created to assess the accuracy of the vegetation types, as mapped for both conifer and hardwood species. The overall accuracy for vegetation classes sampled was 73 percent. Based on the error matrix, decisions were made concerning the directions and percentages of changes for each vegetation class concerned.

Here is an example of how the resulting rules were used to create the input maps for the sensitivity model. The rules were mostly formulated by using the net omission and commission errors within each category. For example, 21 percent of the samples mapped as black oak were photointerpreted to be live oak woodland, while 3 percent of the live oak woodland stands in the map were photointerpreted as black oak. Therefore, in the simulation, we designated that 18 percent of the black oak pixels would be changed to live oak woodland in the map replicates. In the same manner, 17 percent of mixed conifer pixels were changed to black oak, 16 percent of Douglas-fir to live oak woodland, 7 percent of subalpine conifer to mixed conifer, and 4 percent of mixed conifer to live oak woodland.

Since chaparral is so extensive in the San Bernardino forest area, some of the chaparral pixels, if chosen randomly by the model and assigned a forest vegetation type, would land in totally improbable habitat areas. Since southern California Spotted Owls are known to prefer riparian areas, we created a 200 m buffer around streams (John Stephenson, pers. comm.), and the chaparral pixels within that restricted area were used to simulate labeling errors between chaparral and forest classes. Based on estimated commis-sion and omission errors, we estimated a 10 percent net error. The amount of pixels in-cluded in the stream buffer was approximately 50 percent of the

Table 1.—*Error matrix of vegetation class accuracy for the San Bernardino National Forest, California, showing the true class membership of training sites based on photointerpretation, versus the label received in the original map.*

					MAPPED				
	N=227	Black oak	Live oak woodland	Mixed conifer	Jeffrey pine	Douglas fir	Subalpine conifer	Chaparral	Row total
	Black oak	22	1(3%)	8(17%)				2	33
	Live oak woodland	6(21%)	29	2(4%)	0	5(16%)	0	(31%)19	61
	Mixed conifer	0	0	30	2(6%)	0	0	0	32
TRUE CLASS	Jeffrey pine	0	0	2(4%)	30	0	0	0	32
	Douglas fir	0	0	1(2%)	0	27	0	(13%)4	32
	Subalpine conifer	0	0	3(7%)	0	0	27	7	37
	Column total	28	30	46	32	32	27	32	227
	Percent Training Sites Correctly Classified = 165/227 =				**72.69%**				

total pixels for chaparral, so 5 percent of the buffered chaparral pixels were randomly changed to live oak woodland, and another 5 percent to Douglas-fir.

For canopy cover and crown size, the overall accuracy showed poor agreement, particularly for the hardwood species. Specific biases were noted towards class 2 in conifer cover, class 4 in conifer size, and class 3 in hardwood size. Similar vegetation mapping projects have also shown that especially the size estimates derived with these methods are unreliable (Woodcock *et al.* 1994). Also, the sample size per class was quite small, even to develop rough estimates of the direction and magnitude of map error. Therefore, for both canopy and size, it was decided to first add an increase of one class to 10 percent of randomly selected pixels in each class, and then subtract a class from 10 percent of the pixels in each class.

Implementation of the Sensitivity Model

After the habitat value scores were applied to the 60 simulated maps, binary maps were created for each one showing the number and pattern of acceptable habitat pixels using the threshold habitat score of 27. Figure 6 depicts the variation in class area among map iterations as compared to the original number of pixels for mixed conifer, black oak, live oak woodland, and bigcone Douglas-fir. For canopy cover and crown size, the differences are not as great because we changed fewer pixels. Table 2A summarizes the results of these significance tests. The p-value in each case shows that the differences were significant.

In the binary maps of suitable/non-suitable habitat, the simulations added to the number of acceptable habitat pixels in the original map (fig. 7). This is due to the nature of the errors

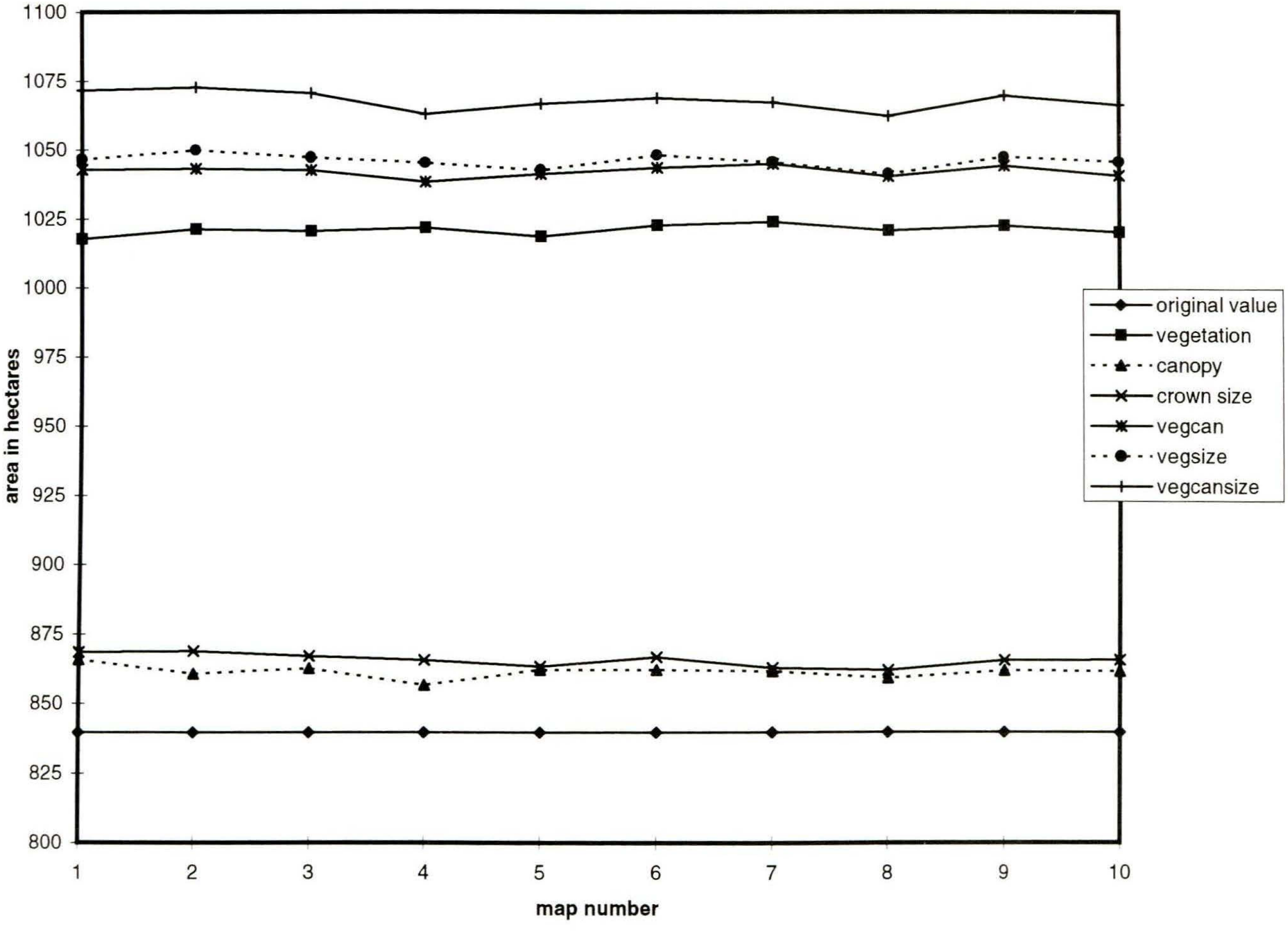

Figure 6.—*Results of sensitivity analysis, San Bernardino National Forest, California: Suitable habitat areas for each corrected change category: Vegetation, canopy cover, and crown size changes; changes in vegetation and canopy cover (vegcan); in vegetation and crown size (vegsize); and in vegetation, canopy cover, and crown size (vegcansize).*

Table 2. Sensitivity analysis results, San Bernardino National Forest, California: (A) Changes in areas of single map categories; (B) Changes in combinations of map categories; (C) The difference in numbers of known owl locations falling within suitable habitat with different types of map corrections (number of pixels with a suitable habitat score ≤ = 27). Original value = 233 pixels. Note: All values are in pixel counts.

Variable	*Original Value*	*Mean*	*Standard Deviation*	*p-value 95% confidence interval*
mixed conifer changes	726487	597603	1084	0.0022
black oak changes	27959	146064	923	0.0022
live oak woodland changes	103259	188888	1367	0.0022
bigcone douglas fir changes	83758	108466.4	828	0.0022
canopy category 10 changes	353770	361334	673	0. 0059
canopy category 20 changes	539994	550838	487	0.0022
canopy category 30 changes	548286	529776	521	0.0059
size category 1 changes	283867	304190	855	0.0022
size category 2 changes	874865	864175	866	0.0059
size category 3 changes	283318	273686	309	0.0022

(A)

Variable	*Original Value*	*Mean*	*Standard Deviation*	*p-value 95% confidence interval*
veg-class changed	335819	408376	717	0.002
canopy % changed	335819	344515	903	0.002
crown size changed	335819	346205	870	0.002
veg & canopy changed	335819	416850	756	0.002
veg & size changed	335819	418354	962	0.002
veg & canopy & size changed	335819	427113	1308	0.002

(B)

Variable	*Mean*	*Standard Deviation*	*p-value 95% confidence interval*
veg-class changed*	233.5	3.35	0.5239
canopy % changed*	234.1	2.59	0.2309
crown size changed*	235.7	2.28	0.0126
veg & canopy changed*	234.2	4.42	0.4738
veg & size changed*	235.4	3.93	0.0577
veg & canopy & size changed*	235.6	5.18	0.2198

(C)

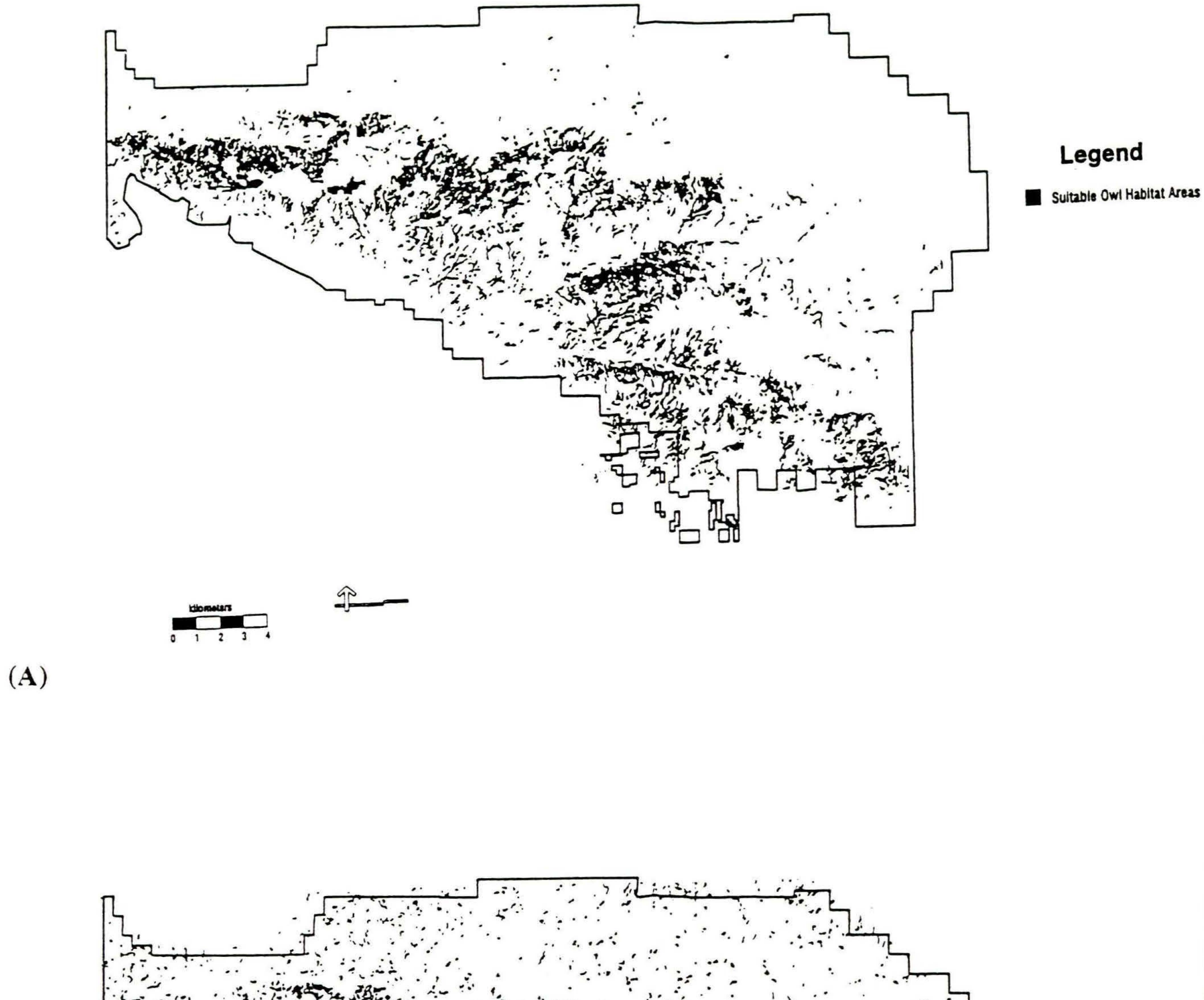
Legend
Suitable Owl Habitat Areas
kilometers
0 1 2 3 4
(A)
Legend
Suitable Owl Habitat Areas
kilometers
0 1 2 3 4
(B)

Figure 7.—*Results of sensitivity analysis: Comparison of binary maps of suitable habitat area (pixels with a suitable habitat score HS ≤ 27). (A) Suitable habitat in original map; (B) Suitable habitat in map resulting from all combinations of map changes.*

in the original map that consisted of omissions from important habitat types. For changes only in canopy cover, this amounted to around 25 ha, with size changes adding slightly more. Changes in vegetation classes consistently added more pixels, with just vegetation class simulations adding at least 175 ha, and increasing with further changes, adding almost 25 more ha per map when all three attributes were altered. Table 2B shows significant differences due to these changes.

We then examined the number of actual owl sighting locations contained in predicted areas of suitable habitat to see if the different combinations of map changes had a significant effect on the number of those locations. The results were not statistically significant in all instances except changes in crown size (table 2C).

Summary of Landscape Pattern Measurements

The various map simulations affected the fragmentation indices significantly, in all of the combinations of vegetation changes (table 3). Only canopy and crown size changes for Patch Size Standard Deviation and canopy changes for the Double Log Fractal Dimension did not change the fragmentation indices significantly. This is interpreted as resulting from the methods employed in this research: we changed fewer pixels for canopy and crown size than for vegetation classes.

DISCUSSION AND CONCLUSIONS

Changes in vegetation class labels, especially combined with changes in canopy and crown size, created landscapes with a greater number of patches, smaller, closer together, with greater variation of size, and less complicated shapes. In weighing these factors, some, such as a greater number of patches that are closer together, and in less complicated shapes, seem to denote a landscape area with a more favorable configuration of Spotted Owl habitat. At the same time, these smaller patches, with less uniform size, seem to suggest an actual pattern of habitat that is more fragmented and possibly unsuited for the long-term survival of the species.

Figure 7 is a binary map of suitable habitat area from the original map as compared to the same showing pixels added by all combined change combinations. The maps show that much of the suitable habitat area added in the simulations is outside of the higher mountainous areas and in the riparian buffer in the chaparral zone. The vegetation class labels were changed to correct estimated map errors, and therefore the majority of pixels added were to black oak, live oak woodland, and Douglas-fir classes. Pixels were lost from higher elevation conifer categories such as mixed conifer and subalpine conifer. This possible incorrect assignment of vegetation classes in the original, or unchanged, forest map could have been caused by the criteria used for life form classification by the USDA Forest Service. The rule that conifer stands were defined as having ≥10 percent of conifer cover (Franklin and Woodcock 1997) caused mixed conifer/hardwood stands to have a primary vegetation class label corresponding to a small percentage of conifer composition.

While riparian areas suitable for Spotted Owl habitat were added in the simulations, the correspondence between numbers of known Spotted Owl locations, and the number predicted from the habitat map, was not significantly increased by adding these areas. Scale could have been a factor in the number of known Spotted Owl locations captured in both the original and corrected, or simulated, maps. Hunter *et al.* (1995) found that spatial scale was a critical factor in finding land cover types that include Spotted Owl nests. The minimum mapping unit of the vegetation map for this research, as represented by the size of each polygon, may have been too large for the accurate measurement of small narrow riparian areas used as potential owl nesting sites. The generalization of vegetation classification within each polygon can miss detecting small topographic features within the landscape that are important as suitable habitat areas. Bowser (1996) concluded that the resolution of GIS map layers can impose an unrealistic decision-scale when representing the ecological restraints of an animal. In a case such as this, where the minimum mapping unit of the map is suspected of not identifying potentially important habitat features, further testing could be done. A sample area could be chosen, and the automated polygon delineation redone at a smaller scale before the life form classification. Then the mapping process could be completed and the sensitivity analysis redone. A smaller minimum mapping unit, however, may introduce cost or computer space constraints due to increases in computer usage.

Table 3.—*Sensitivity analysis results: differences in landscape fragmentation indices between original and corrected maps with different types of map changes.*

Variable	*Original Value*	*Type of Map Correction*	*Mean*	*Standard Deviation*	*p-value 95% confidence interval*
SIZE					
Mean Patch Size	18 hectares	vegetation	10.13	0.13	0.0022
		canopy	17.68	0.16	0.0025
		size	17.51	0.16	0.0022
		veg-can	10.12	0.14	0.0022
		veg-size	10.13	0.14	0.0022
		veg-can-size	10.12	0.15	0.0022
Patch Size Standard Deviation	87 hectares	vegetation	55.80	3.38	0.0022
		canopy	87.32	1.71	0.7695
		size	86.01	4.25	0.7695
		veg-can	55.97	3.02	0.0022
		veg-size	56.36	4.00	0.0022
		veg-can-size	56.49	3.30	0.0022
SHAPE					
Double Log Fractal Dimension	1.468	vegetation	1.40	0.00	0.0025
		canopy	1.47	0.00	0.4124
		size	1.47	0.00	0.0461
		veg-can	1.40	0.00	0.0025
		veg-size	1.40	0.00	0.0025
		veg-can-size	1.40	0.00	0.0025
DISTRIBUTION					
Mean Nearest-Neighbor Distance	159.58 meters	vegetation	156.03	3.20	0.0022
		canopy	161.46	2.03	0.0137
		size	170.84	4.38	0.0022
		veg-can	156.21	3.55	0.0039
		veg-size	156.22	2.53	0.0039
		veg-can-size	154.85	2.80	0.0039
Nearest -Neighbor Standard Deviation	365.38 meters	vegetation	212.30	5.90	0.0022
		canopy	296.85	7.93	0.0022
		size	324.15	29.76	0.0059
		veg-can	203.97	6.60	0.0022
		veg-size	204.37	7.15	0.0022
		veg-can-size	197.12	5.99	0.0022
DENSITY					
Number of Patches	1159	vegetation	2519.40	31.19	0.0059
		canopy	1218.10	9.07	0.0059
		size	1235.90	11.06	0.0059
		veg-can	2575.00	34.04	0.0022
		veg-size	2582.10	33.39	0.0022
		veg-can-size	2637.90	35.65	0.0022
Patch Density	5.52 per 100 hectare	vegetation	9.87	0.13	0.0022
		canopy	5.66	0.05	0.0059
		size	5.71	0.05	0.0022
		veg-can	9.88	0.14	0.0022
		veg-size	9.88	0.13	0.0022
		veg-can-size	9.88	0.14	0.0022

Also, image classification may not be able to resolve forest type and structure at this finer scale, and time-consuming and costly photo-interpretation would be required to refine the more detailed habitat map.

If the maximum amount of habitat areas predicted were preserved, based on the corrections made for estimated map errors in vegetation, canopy cover, and crown size class, the effect on the long-term survival of metapopulations of the Spotted Owl in this area is not known. The smaller patches shown in the corrected maps, closer together, and in greater density (as shown by the fragmentation statistics), still might be valuable as marginal habitat, and possibly useful for dispersal. They could be big enough for nesting, surrounded by small areas valuable for foraging. Previously, we mentioned the variability in researchers' determinations of ideal territory size for the California Spotted Owl, with an overall estimation of 200-1,000 ha depending on elevation and prey density (Verner *et al.* 1992). While the importance of forest composition and structure are known (Verner *et al.* 1992), the effect of habitat fragmentation, both present and projected, is the subject of ongoing research using population model simulations being developed by Schumaker (in press) and Stephenson (Master's thesis in progress).

The changes made in the sensitivity analysis attempted to correct error in map classification by reassigning specified percentages of pixels among classes. This should have made the resulting corrected maps more accurate both in themselves, and in the estimation of possible habitat area. The map replications represented different possible realizations of the spatial distribution of map classes. The magnitude and direction of error assessed for the original map indicates that owl habitat area is underestimated, specifically in representing marginal habitat. The simulated corrections indicate that this additional habitat is in small patches outside the core habitat area, but this may be due to one of the assumptions made in generating the map changes (randomly choosing stands or segments for label reassignment). This may not have been a reasonable assumption. Errors in a mapping process tend to be spatially autocorrelated, and would occur along ecotonal boundaries, potentially forming larger, more clustered habitat patches. This could be simulated by making vegetation class changes based on parameters related to the distribution of these classes, such as the combination of slope, aspect, and elevation used in predicting the forest cover type from terrain rules, or proximity to known owl locations. To implement this suggestion, we would recommend that: (1) the gradient models be used to alter the probability of the location of the addition or subtraction of pixels in the sensitivity model for different vegetation types; and (2) buffers be created around ecotonal boundaries, thus creating an area for possible habitat corrections more reflective of realistic error possibilities.

An additional method, based on proximity to known spotted owl locations, would be to develop a trend surface model to describe the locational trends in spotted owl habitat use (Periera and Itami 1991). This could be used to revise the probabilities of a pixel being suitable for owl habitat based on prior knowledge of spotted owl habitat preferences. As we stated above, the eventual consequences of these differences in the estimated habitat area and patterns on population viability can only be explored via population modeling, and are especially critical because of controversy about habitat requirements and configuration.

The utility of this study could also be improved by increasing the percentage of change for canopy and crown size, and making those among-class changes reflective of the estimated errors. Changing 10 percent of each class may have been too conservative for the low accuracy of the data found in the original canopy and crown size maps, and did not reflect the labeling bias that was observed. Therefore, the results of the simulations for size and cover labels are less useful than those for vegetation class changes.

There is a gap between the subjectivity found in decision-making processes based on this kind of map data, and the objectivity needed for scientific methods. Sensitivity analysis can be a useful framework within which to re-scale and re-weigh the various factors involved. Geographic Information Systems are increasingly being used in conservation biology and wildlife management for habitat modeling, population simulation modeling, and reserve design, and are appropriate for the repetition and re-assessment of the changes produced from a sensitivity analysis model. Different realizations of mapped distributions can be both visually and statistically compared and adjusted as needed. Careful research based on the output of these simulations is a further step in closing that gap.

While GIS is an efficient and "...virtually error-free system for manipulating map data, the data being processed are often of variable precision" (Openshaw 1989). Models of error need to be developed and used routinely or the usefulness of GIS will be compromised (Chrisman 1989, Veregin 1989). User awareness as to the extent of error in spatial databases needs to be improved, and policy-makers whose decisions are based on products of data transformation processes should have a more accurate estimate of their reliability (Lanter and Veregin 1992, Openshaw 1989). Management decisions made about species such as the California Spotted Owl are critical to its survival, and must often be made before its habitat associations can be fully determined. Sensitivity analysis can be further developed to supply a knowledge of the reliability of the assumptions that must be made.

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LITERATURE CITATIONS

Alexander, E.R. 1989. Sensitivity analysis in complex decision models. Journal of the American Planning Association, Summer: 323-333.

Anderson, M.C.; Mahato, D. 1995. Demographic models and reserve designs for the California Spotted Owl. Ecological Applications. 5(3): 639-647.

Anderson, S.H.; Gutzwiller, K.J. 1994. Habitat evaluation methods. In: Bookhout, T.A., ed. Research and management techniques for wildlife and habitats. Bethesda, Maryland: The Wildlife Society: 592-622.

Beck, T.W.; Gould, G.I. 1992. Background and the current management situation for the California Spotted Owl. In: Verner, J.; McKelvey, K.S.; Noon, B.R.; Gutierrez, R.J.; Gould, G.I.; Beck, T.W., eds. The California Spotted Owl: a technical assessment of its current status. Gen. Tech. Rep. PSW-133. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station: 37-54.

Bowser, G. 1996. Integrating ecological tools with remotely sensed data: modeling animal dispersal on complex landscapes. World Wide Web page: http://www.ncgia.ucsb.edu/conf/sant_fe_cdom/sf_papers/gillian_bowserncgia2.html

California Spotted Owl Recovery Plan. 1994. Hearing before the Subcommittee on National Parks, Forests, and Lands. One Hundred Fourth Congress. Serial No. 104-22. Washington, DC: U.S. Government Printing Office.

Chalk, D.E. 1986. Summary: development, testing, and application of wildlife-habitat models: the researcher's viewpoint. In: Verner, J.; Morrison, M.L.; Ralph, C.J., eds. Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. Madison, Wisconsin: The University of Wisconsin Press: 155-156.

Chrisman, N.R. 1989. Modeling error in overlaid categorical maps. In: Goodchild, M.; Gopal, S., eds. The accuracy of spatial databases. London: Taylor & Francis: 21-34.

Doak, D.F. 1989. Spotted Owls and old growth logging in the Pacific Northwest. Conservation Biology. 3(4): 389-396.

Durant, S.M.; Mace, G.M. 1994. Species differences and population structure in population viability analysis. In: Olney, P.J.S.; Mace, G.M.; Feistner, A.T.C., eds. Creative conservation: interactive management of wild and captive animals. London: Chapman & Hall: 67-91.

Forest Service, Region 5. 1994. Forest inventory analysis user's guide. Sacramento, CA: U.S. Department of Agriculture, Forest Service, Region 5 Remote Sensing Laboratory, Franklin, J.; Stephenson, J. 1996. Integrating GIS and remote sensing to produce regional vegetation databases: attributes related to environmental modeling. World Wide Web page: http://bbq.ncgia.ucsb.edu:80/conf/sf_papers/franklin_janet/my_paper.html.

Franklin, J.; Woodcock, C.E. 1997. Multiscale vegetation data for the mountains of southern California: spatial and categorical resolution. In: Quattrochi, D.A.; Goodchild, M.F., eds. Scale in remote sensing and GIS. Boca Raton, Florida: CRC/Lewis Publishers Inc. In press.

Goodchild, M.F. 1994. Integrating GIS and remote sensing for vegetation analysis and modeling: methodological issues. Journal of Vegetation Science. 5: 615-626.

Greif, N. 1995. Is habitat modification that kills or injures endangered wildlife a prohibited taking under the Endangered Species Act? Natural Resources Journal. 35(1): 189-199.

Gutierrez, R.J.; Pritchard, J. 1990. Distribution, density, and age structure of Spotted Owls on two southern California habitat islands. Condor. 92: 491-495.

Gutierrez, R.J.; Franklin, A.B.; LaHaye, W.S. 1995. Spotted Owl (*Strix occidentalis*). In: Poole, A.; Gill, F., eds. The birds of North America, No. 179. Philadelphia: The Academy of Natural Sciences, and Washington, DC: The American Ornithologists' Union.

Heinen, J.T.; Lyon, J.G. 1989. The effects of changing weighting factors on wildlife habitat index values: a sensitivity analysis. Photogrammetric Engineering and Remote Sensing. 55: 1445-1447.

Hunter, J.E.; Gutierrez, R.J.; Franklin, A.B. 1995. Habitat configuration around Spotted Owl sites in northwestern California. Condor. 97: 684-693.

Jensen, J.R. 1996. Introductory digital image processing: a remote sensing perspective. 2d ed. New Jersey: Prentice Hall.

LaHaye, W.S.; Gutierrez, R.J. 1994. Big Bear spotted owl study, 1993. Nongame bird and mammal section report 94-3. State of California Department of Fish and Game.

LaHaye, W.S.; Gutierrez, R.J.; Akcakaya, H.R. 1994. Spotted Owl metapopulation dynamics in southern California. Journal of Animal Ecology. 63: 775-785.

Lamberson, R.H.; Noon, B.R.; Voss, C.; McKelvey, K.S. 1994. Reserve design for territorial species: the effects of patch size and spacing on the viability of the Northern Spotted Owl. Conservation Biology. 8(1): 185-195.

Lande, R. 1988. Demographic models of the Northern Spotted Owl (*Strix Occidentalis occidentalis*). Oecologia. 75: 601-607.

Lanter, D.P.; Veregin, H. 1992. A research paradigm for propagating error in layer-based GIS. Photogrammetric Engineering and Remote Sensing. 58(6): 825-833.

Lodwick, W.A.; Monson, W.; Svoboda, L. 1990. Attribute error and sensitivity analysis of map operations in geographical information systems. International Journal of Geographical Information Systems. 4: 413-428.

Lowry, J.H., Jr.; Miller, H.J.; Hepner, G.F. 1995. A GIS-based sensitivity analysis of community vulnerability to hazardous contaminants on the Mexico/U.S. border. Photogrammetric Engineering and Remote Sensing. 61(11): 1361-1370.

McGarigal, K.; Marks, B. 1994. Fragstats: spatial pattern analysis program for quantifying landscape structure. (Software application) Forest Science Department, Oregon State University, Corvallis, OR 97331.

Moffat, A.S. 1994. Theoretical ecology, winning its spurs in the real world. Science. 263: 1090-1092.

Morrison, M.L.; Marcot, B.G.; Mannan, R.W. 1992. Development of predictive models, in wildlife-habitat relationships, concepts and applications. Madison, Wisconsin: The University of Wisconsin Press.

Noon, B.R.; McKelvey, K.S. 1992. Stability properties of the Spotted Owl metapopulation in southern California. In: Verner, J.; McKelvey, K.S.; Noon, B.R.; Gutierrez, R.J.;

Gould, G.I.; Beck, T.W., eds. The California Spotted Owl: a technical assessment of its current status. Gen. Tech. Rep. PSW-133. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station: 187-206.

Openshaw, S. 1989. Learning to live with errors in spatial databases. In: Goodchild, M.; Gopal, S., eds. The accuracy of spatial databases. London: Taylor and Francis: 263-276.

Periera, J.M.C.; Itami, R.M. 1991. GIS-based habitat modeling using logistic multiple regression: a study of the Mt. Graham red squirrel. Photogrammetric Engineering and Remote Sensing. 57(11): 1475-1486.

Ripple, W.J.; Bradshaw, G.A.; Spies, T.A. 1991. Measuring forest landscape patterns in the Cascade Range of Oregon, USA. Biological Conservation. 57: 73-88.

Roberts, C.K. 1993. California Spotted Owl inventory and demographic study, Sequoia and Kings CanyonNational Parks: final 1988-89. Tech. Rep. 1993 - 4. State of California Department of Fish and Game.

Schumaker, N. In press. A simulation modeling approach to quantifying landscape quality.

Stephenson, J. 1991. Spotted Owl surveys on the National Forests of southern California: a status report and recommendations for the future. San Bernardino, CA: U.S. Department of Agriculture, Forest Service, 13 p.

Stoms, D.M.; Davis, F.W.; Cogan, C.B. 1992. Sensitivity of wildlife habitat models to uncertainties in GIS data. Photogrammetric Engineering & Remote Sensing. 6: 843-850.

Usher, M.B. 1987. Effects of fragmentation on communities and populations: a review with applications to wildlife conservation. In: Saunders, D.A.; Arnold, G.W.; Burbidge, A.A.; Hopkins, A.J.M., eds. Nature conservation: the role of remnants of native vegetation. Australia: Surrey, Beatty, and Sons: 103-121.

Veregin, H. 1989. Error modeling for the map overlay operation. In: Goodchild, M.; Gopal, S., eds. The accuracy of spatial databases. London: Taylor & Francis: 3-18.

Verner, J.; Taylor, R.J. 1992. Future directions for the California spotted owl effort. In: Verner, J.; McKelvey, K.S.; Noon, B.R.; Gutierrez, R.J.; Gould, G.I.; Beck, T.W., eds. The California Spotted Owl: a technical assessment of its current status. Gen. Tech. Rep. PSW-133. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station: 27-36.

Verner, J.; McKelvey, K.S.; Noon, B.R.; Gutierrez, R.J.; Gould, G.I.; Beck, T.W. 1992. In: Verner, J.; McKelvey, K.S.; Noon, B.R.; Gutierrez, R.J.; Gould, G.I.; Beck, T.W., eds. The California Spotted Owl: a technical assessment of its current status. Gen. Tech. Rep. PSW-133. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. 285 p.

Wilcove, D.S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. Ecology. 66: 1211-1214.

Woodcock, C.E.; Collins, J.; Gopal, S.; Jakabhazy, V.D.; Li, X.; Macomber, S.; Ryherd, S.; Harward, V.J.; Levitan, J.; Wu, Y.; Warbington, R. 1994. Mapping forest vegetation using Landsat TM imagery and a canopy reflectance model. Remote Sensing of Environment. 50: 240-254.

Yaffee, S.L. 1994. The wisdom of the Spotted Owl: policy lessons for a new century. Washington, DC: Island Press.

Banding of *Asio* Owls in south-central Saskatchewan

C. Stuart Houston[1]

Abstract.—During a long-term Great Horned Owl (*Bubo virginianus*) banding program, 1946-1996, there were opportunities to band 507 Long-eared Owls (*Asio otus*) and 246 Short-eared Owls (*Asio flammeus*). No less than 35.1 percent of the Long-eared Owls and 63.5 percent of the Short-eared Owls were banded in two unusual years, 1960 and 1969, after *Microtus* had proliferated under swaths of grain that lay unharvested beneath the snow. Such numbers are strong but not conclusive support for nomadism. Five Long-eared Owls were recovered (1 percent of bandings) but no Short-eared Owls, and there have been no recoveries from the last 280 Long-eared Owls banded since 1968.

METHODS

During a long-term banding program with visits to 3,105 successful nests of the Great Horned Owl (*Bubo virginianus*) in 486 different 10-minute blocks of latitude and longitude across Saskatchewan, and resulting from publicity and interest thereby generated, there were occasional, incidental opportunities to learn of nests of other owl species. I banded 501 nestlings of the Long-eared Owl (*Asio otus*) in 139 successful nests, plus two fledglings, and 244 nestlings of the Short-eared Owl (*Asio flammeus*) in 78 nests, plus one fledgling. In addition, I banded four adult female Long-eared Owls and one Short-eared Owl which remained on their nests to protect young. The Short-eared Owl nests were found on stubble during farm operations by farmers who knew of my interest in banding Great Horned Owls. The Long-eared Owl nests were found in roughly equal numbers by interested farmers and by birders. The banding visits kept me busy and I made no formal nest searches myself.

I used the 20 years, 1966-1985, of intensive data collection by members of the Saskatoon Nature Society (SNS) in the Saskatoon area, 51°30' to 52°30' N. and 106°00' to 107°30' W., as an additional, semi-independent test of numerical fluctuations. Rob Johanson analyzed computerized entries of 624 monthly sighting cards of Short-eared Owls recorded by up to 50 observers 1966-1985. I analyzed, manually, the 154 SNS record cards for the Long-eared Owl, 1966-1985, and entered them into a database for the first time.

RESULTS

Years of Vole Abundance

At least one or two nests of the Long-eared Owl were visited each year in 34 different years, but nests of the Short-eared Owl were located in only 11 years (table 1). In both species, banding was concentrated in 2 years, 1960 and 1969, when rodents, chiefly *Microtus* and *Peromyscus*, proliferated beneath the snow under swaths of unharvested grain from the previous autumn. No numerical data are available for rodents, but in both 1960 and 1969 a number of farmers reported that they had never before seen so many in the fields, supporting my own field observations. About 63.5 percent of my lifetime Short-eared Owl and 35.1 percent of my Long-eared Owl banding took place during those 2 years. In 3 other years, 1964, 1966 and 1967, when rodents appeared unusually plentiful, Long-eared Owls were also common, as were Short-eared Owls in 1964 and 1967.

Two other Saskatoon banders took advantage of the surge in numbers of Long-eared Owls, centering on 1969. Each conducted nest searches of his own. R.E. Gehlert banded 12 Long-eared Owls in four nests in 1968 and 43 in nine nests in 1969, the year D.W.A. Whitfield banded 13 in two nests.

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Table 1.—*Long-eared (LEOW) and Short-eared (SEOW) Owls banded by C.S. Houston in south-central Saskatchewan.*

Year	LEOW	# nests	Yng/ nest	Adult Fledg	Recov	SEOW	# nests	Yng/ nest	Adult Fledg
1946	0			F					
1952	5	1	5.0			0			
1953	0					0			
1954	0					0			
1955	0					0			
1956	0					0			
1957	0					0			
1958	5	1	5.0			0			
1959	12	4	3.0			0			
1960	73	18	4.1	A	1	68	22	3.1	A
1961	0					0			
1962	0					0			
1963	0					0			
1964	28	7	4.0	A		16	7	2.3	
1965	0			A		0			
1966	65	20	3.3		2	0			
1967	34	10	3.4	A	2	15	4	3.8	
1968	16	4	4.0			0			
1969	103	28	3.7			87	26	3.3	
1970	0					0			F
1971	14	4	3.5			0			
1972	29	7	4.1			0			
1973	6	2	3.0			0			
1974	5	1	5.0			39	13	3.0	
1975	9	2	4.5			3	1	3.0	
1976	3	1	3.0			0			
1977	3	1	3.0			0			
1978	2	1	2.0			3	1	3.0	
1979	7	2	3.5			0			
1980	6	2	3.0			0			
1981	3	1	3.0			0			
1982	0					0			
1983	17	5	3.4			8	2	4.0	
1984	8	2	4.0			0			
1985	3	1	3.0			0			
1986	0					2	1	2.0	
1987	2	1	2.0			0			
1988	4	1	4.0			0			
1989	6	2	3.0			0			
1990	2	1	2.0			0			
1991	6	2	3.0	F		0			
1992	9	3	3.0			0			
1993	4	1	4.0			3	1	3.0	
1994	9	2	4.5			0			
1995	0					0			
1996	3	1	3.0			0			
Total	501	140	3.6	6	5	244	78	3.1	2
2best	176					155			
	35.1%	None from last 280 banded				63.5%			
Recoveries					1.0%				0.0%

In all 4 years of abundance, Short-eared Owl nests were found in open stubble, as many as two nests per 65 ha, on farms where none had been seen in previous years. In most intervening years, Short-eared Owl sightings were largely restricted to spring and fall migration and our farmer nest-finders reported no nests. It is of interest that Northern Harriers (*Circus cyaneus*) were also more abundant in 1960 and 1969, with 177 of my 400 bandings (42 percent) of this 'mouse-driven' hawk (Hamerstrom 1986) restricted to those 2 years.

Food

Uneaten prey items in nests of both species have almost exclusively consisted of *Microtus* and *Peromyscus*. I know of no pellet analysis or other formal study of food items for either species in Saskatchewan.

Nest Sites

Short-eared Owl nests were found almost exclusively in swathed stubble from the previous year's grain crop (e.g., wheat, oats, barley); two were in *Symphoricarpos* cover. No nests were found in 'typical' sites in dry, grassy meadows, where, in contrast to stubble, there is enough vegetation to conceal the incubating female (Holt and Leasure 1993). Clark (1975) reported 63 nests, of which 35 were in grassland, nine in alfalfa hayland, four in low perennial vegetation, and only 15 (24 percent) in grain stubble. The absence of any recoveries from my banding raise the possibility that the young on stubble in the absence of appreciable cover were vulnerable to predation.

Long-eared Owls used stick nests of other species, usually the American Crow (*Corvus brachyrhynchos*), but on occasion a roofed or partially roofed nest of a Black-billed Magpie (*Pica pica*). In 1969, there were two instances where two nests and once, three nests, were present in adjacent aspen copses, 100 or 150 m from the first nest found.

Brood Size

Short-eared Owl brood size (n=78) at the banding visit averaged 3.1 young, but this number is not representative of initial clutch size because: the young at 12 to 18 days begin to disperse on foot in different directions up to 200 m from the nest, owlets are of different ages so that the oldest may leave the nest before the youngest is large enough to band, predation of conspicuous ground nests is high, and some owlets die from starvation. In 1960, a peak vole year, the first six nests of the season contained 43 young, of which only 22 were of an appropriate size for banding. A striking example of possible parental cannibalism to achieve brood reduction within the competence of the surviving adult was seen near Theodore, Saskatchewan. One evening there were six healthy-looking young in the nest; by the next morning, 4 June 1960, one adult had been killed by flying into a high tension electricity transmission line, and the remaining parent was feeding the dismembered parts of the three smallest to the three oldest. The largest clutch included seven young and four eggs, in a nest in stubble at Greenan, Saskatchewan, 28 May 1966; this ties the North American record for the largest clutch ever reported (Holt and Leasure 1993).

Long-eared Owl brood size (n=139) at banding age averaged 3.6 young per nest, exclusive of five owlets unbanded because they were too small to band. In the first high vole year, 1960, the mean was 4.1 young per successful nest (n=18); that year, one nest had six young, four nests had five young each, nine pairs raised four young, three nests had three, and only one nest had two young. There was also one nest with six young in 1964 and again in 1966. The combined banding of Gehlert and Whitfield in 1968 and 1969 averaged 4.5 young per successful nest, Gehlert having two nests that produced seven young to banding age, and Whitfield one such nest. A Long-eared Owl nest with nine eggs on 25 May 1969 was the largest clutch I encountered; this nest subsequently failed.

SNS Record Cards

Short-eared Owl

Over-wintering occurred particularly in the high vole year of 1969. Prior to the concerted study there were retrospective SNS card entries for sightings throughout January and February in 1960, and during the intensive study, one sighting in early January 1972. There was one nest in 1964. There were two nests in 1966, one in 1967, 16 in 1969, and no nests between 1970 and 1985, inclusive. Most observations were during spring migration and a smaller number in fall migration; there were sightings throughout all months in 1968-1969 but only seven observations in November and December of all other years combined. The number of Short-eared Owl observations is shown by year in figure 1.

Long-eared Owl

SNS record cards in 1966 recorded 32 visits to 20 Long-eared Owl nests or broods and only seven sightings away from a nest; in 1967, 17 visits to 11 nests, one found dead and one sighting away from a nest; in 1968, eight visits to four nests and one sighting; in 1969, 43 visits to 26 nests, two found dead and five sightings, including the latest fall date of 5 October. There were two nests in 1971, seven nests in 1972, two nests in 1973, with no sightings away from a nest in these 3 years. One nest each in 1974, 1975, and 1980, a single sighting in 1977 representing the earliest spring arrival date of 24 March, two nests each in 1983 and 1984, and another six sightings away from known nests, commonly after the nesting period. While effort may have diminished somewhat in these later years, there were no Long-eared Owl sightings reported in 1976, 1979, 1981, and 1982.

Recoveries

The number of recoveries has been disappointing: five (1 percent) from 507 Long-eared Owls (none from the last 280 banded) and zero from the 246 Short-eared Owls banded. Long-eared

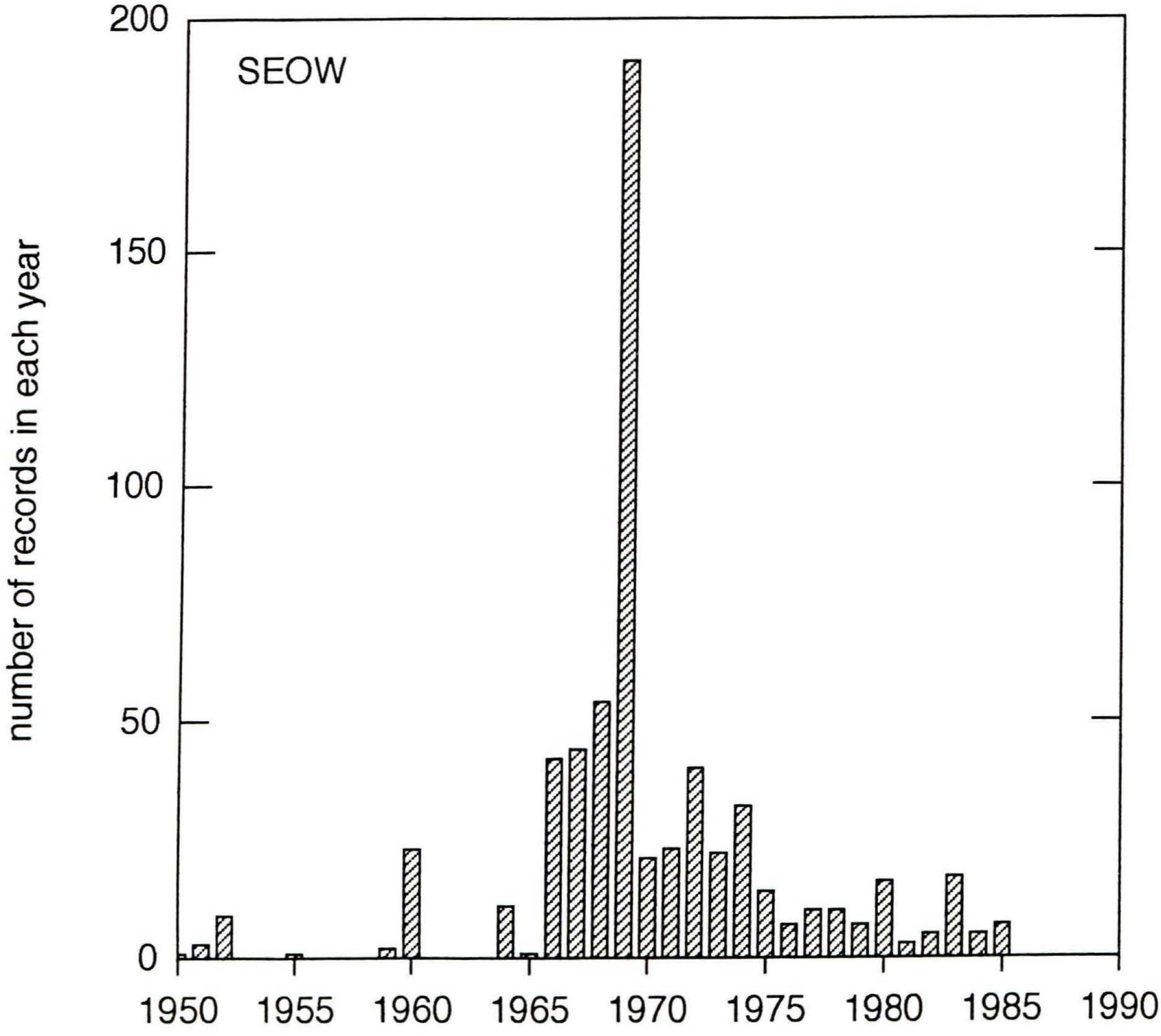

Figure 1.—*Numbers of Short-eared Owl observation records, 1950-1990, from the Saskatoon Nature Society record cards.*

Table 2.—*Recoveries of Long-eared Owls banded in south-central Saskatchewan.*

Banded	June	Lat.	Long.	Recovered			Age	Lat.	Long.	Distance *km*	Direction *Degrees*
Saltcoats	1960	510	1020	Found dead	Ejutla,Oaxaca	ca. 1960	0 yr	162	962	3890	170
Grandora	1966	520	1070	Found dead	Billings, MT	Feb. 67	0 yr	454	1083	715	190
Grandora	1966	520	1070	Found dead	Corwith, IA	Apr. 69	2 yr	425	935	1420	130
Grandora	1967	520	1070	In trap	Russell, Man	June 69	2 yr	505	1005	445	104
Saskatoon	1967	520	1064	Found dead	Clarksdale, MS	Dec. 72	5 yr	341	903	2370	140

Owls have been recovered in Manitoba; Iowa; Montana; Mississippi; and Oaxaca, Mexico, at distances of 445 to 3,890 km from the banding site, from 0 to 5 years after banding, with no local recoveries (table 2).

DISCUSSION

It has long been known that populations and reproductive success of Short-eared Owls and Long-eared Owls are tied to the density of small mammals, often *Microtus* voles (Holt and Leasure 1993, Marks *et al.* 1994), and that the Long-eared Owl is nomadic, especially in Europe (Marks *et al.* 1994).

In contrast to the reasonably stable annual populations of the Long-eared Owl in western Montana and Idaho (e.g., Marks 1986), in most years both *Asio* species are rather thinly scattered breeders throughout south-central Saskatchewan. There have been years when groups of keen Saskatoon birders have not sighted a single Long-eared Owl. Thus it is a noteworthy surprise when, in rare, irregularly-spaced years, adult owls appear suddenly in numbers in response to a bonanza of small mammals or rodents. The obvious question is: Where do the owls come from? One can only speculate. In the case of the Short-eared Owl, migrant owls are seen every spring, some of which may be destined to nest on tundra 1,000 km or more farther north; one might speculate that in response to food abundance some of them stop in Saskatchewan to nest. Perhaps in both species some are year-old owls which would not have bred without abundant prey to stimulate the breeding impulse. Whatever the mechanism, my somewhat casual observations offer strong but indirect evidence that high *Microtus* populations do result in major increases in the breeding populations and productivity of both species of *Asio* owl and of the Northern Harrier. Indeed, from this informal study one might conjecture that nomadism of both *Asio* owls is more pronounced in Saskatchewan than has been documented elsewhere in North America.

Although trends are difficult to quantify because of extreme cyclical variations, there has been a substantial decline in the sightings of Short-eared Owls in south-central Saskatchewan since the 1970s, perhaps part of the general decline in numbers and productivity of many species of grassland birds (Houston and Schmutz 1997). Long-eared Owl sightings and bandings have decreased since the late 1960s and early 1970s. The secretiveness of the Long-eared Owl is evident from the marked paucity of sightings away from active nests.

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LITERATURE CITATIONS

Clark, R.J. 1975. A field study of the Short-eared Owl *Asio flammeus* (Pontoppidan) in North America. Wildlife Monograph. 47: 1-67.

Holt, D.W.; Leasure, S.M. 1993. Short-eared Owl (*Asio flammeus*). In: Poole, A.; Gill, F., eds. The birds of North America, No. 62. Philadelphia, PA: The Academy of Natural Sciences; Washington, DC: The American Ornithologists' Union.

Hamerstrom, F. 1986. Harrier, hawk of the marshes: the hawk that is ruled by a mouse. Washington, DC: Smithsonian Institution Press.

Houston, C.S.; Schmutz, J.K. 1997. Changes in Canadian grassland bird populations (Proceedings of Grassland conference, Tulsa, 27-28 October 1995). Journal of Field Ornithology (suppl.) (in press).

Marks, J.S. 1986. Nest-site characteristics and reproductive success of Long-eared Owls in southwestern Idaho. Wilson Bulletin. 98: 547-560.

Marks, J.S.; Evans, D.S.; Holt, D.W. 1994. Long-eared Owl (*Asio otus*), In: Poole, A.; Gill, F., eds. The birds of North America, No. 133. Philadelphia, PA: The Academy of Natural Sciences; Washington, DC: The American Ornithologists' Union.

Black-flies and *Leucocytozoon* spp. as Causes of Mortality in Juvenile Great Horned Owls in the Yukon, Canada

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ABSTRACT.—Black fly feeding and infection with the blood parasite *Leucocytozoon* spp. caused mortality in juvenile Great Horned Owls (*Bubo virginianus*) in the Yukon, Canada during 1989-1990. The mortality occurred during a year of food shortage corresponding with the crash in snowshoe hare (*Lepus americanus*) populations. We postulate that the occurrence of disease was mediated by reduced food availability.

Rohner (1994) evaluated the numerical response of Great Horned Owls (*Bubo virginianus*) to the snowshoe hare (*Lepus americanus*) cycle from 1988 to 1993 in the Kluane Lake area of southwestern Yukon, Canada. The survival of juvenile owls was very high during 1989 and 1990, both years of abundant hare populations. Survival decreased in 1991, the first year of the snowshoe hare population decline (Rohner and Hunter 1996). Monitoring of nest sites combined with tracking of individuals by radio-telemetry provided us with carcasses of 28 juvenile owls found dead during 1990 and 1991 (Rohner and Doyle 1992). Although we observed a variety of causes of death in these carcasses including trauma and bacterial infections, 13 of the 28 owls died from severe anemia, dehydration and extensive skin lesions attributed to feeding by ornithophilic black flies (Diptera: Simulidae) and in several birds, internal lesions caused by heavy concurrent infections with *Leucocytozoon* spp. (Rohner and Hunter 1996, Hunter *et al.* 1997). This was the first record of black flies from Great Horned Owls and provided evidence of black flies as potential pathogens for young owls (Hunter *et al.* 1997).

Black flies are abundant throughout northwestern North America. Of the 70 species of black flies identified from Alaska, USA and the Yukon Territory, Canada, 36 percent are ornithophilic, 39 percent mammalophilic and 25 percent autogenous (Currie 1997). Numerous female black flies were obtained from the carcasses of the juvenile owls, but only 45 of these were sufficiently well preserved for identification. They belonged to four taxa as follows: *Helodon* (*Distosimulium*) *pleuralis* (Malloch), 1; *Helodon* (*Parahelodon*) *decemarticulatus* (Twinn), 3; *Simulium* (*Eusimulium*) *aureum* Fries complex, 3; and *Simulium* (*Eusimulium*) *canonicolum* (Dyar and Shannon) complex, 38 (Hunter *et al.* 1997).

Black flies are pool feeders that penetrate the skin and produce small craterous lesions using a slashing or biting action involving the stylets and labium (Sutcliffe and McIver 1984). Black fly saliva containing anticoagulants, enzymes and histamine, is mixed with the blood preventing clotting until it is ingested by the fly. Black fly bites cause localized tissue damage and if the number of feeding flies is sufficient, they may produce a blood-loss anemia. In addition, the host's reaction to fly attacks may include systemic illness, allergic reactions or even death; these reactions presumably mediated by histamine. Harwood and James (1979) refer to a systemic reaction to black fly bites in humans known as "black fly fever" characterized by headaches, fever, nausea, adenitis, generalized dermatitis, and allergic asthma. In Alberta and Saskatchewan (Canada), intense black fly attacks have caused hysteria, systemic disease, and mortality in cattle (Fredeen 1969, Harwood and James 1979). The pathogenicity of black flies for birds has not been well established. Edgar (1953) reported egg production drops in laying

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chickens tormented by black flies. We could only find a single report of black fly induced pathology in raptorial birds. S. Cain (unpubl. data) observed mortality and premature evacuation of nests by Red-tailed Hawk (*Buteo jamaicensis*) chicks in Wyoming (USA) due to black fly attacks. Black flies are also the main vector for the blood parasite *Leucocytozoon* spp.

Although *Leucocytozoon* spp. can be a serious pathogen in immunologically naive captive or domestic waterfowl, turkeys and chickens (Bennett *et al.* 1993), rarely has it been associated with clinical disease or mortality in wild birds (Herman *et al.* 1975). *Leucocytozoon* spp. infection is common in raptorial birds (Peirce 1981) but documentation of clinical disease and mortality is lacking. The fledgling owls in our study had massive parasitemias and widespread tissue lesions associated with concurrent *Leucocytozoon* spp. infection which we believe contributed to the mortality.

Interestingly, mortality from parasitism only occurred in 1991, the year of the crash in snowshoe hare populations. We have no reason to believe that the owls were not equally parasitized in the previous years of the study, yet in these years clinical disease or mortality due to parasitism was not observed.

We suspect that almost every northern Great Horned Owl chick is exposed to black flies and that most become infected with *Leucocytozoon* spp. Under normal conditions and during years of adequate food supply, as occurred in 1989 and 1990, young birds were able to successfully fight infection, recover from the anemia and fledgling survival remained high. We propose that the occurrence of clinical disease and mortality in 1991 was mediated by reduced food availability and possibly other factors.

Most wildlife managers recognize that disease is endemic in wildlife populations, but there is a tendency to think of disease in terms of individual mortality events or isolated dieoffs. Our understanding of the subclinical effects of disease on individuals or populations is very limited. There is an increasing number of reports demonstrating that subclinical disease in wildlife may affect biological processes such as predator avoidance (Hudson *et al.* 1992, Temple 1987) or reproductive success by influencing mate selection (discussed by Clayton 1991), clutch size (Rohner 1994, Korpimäki *et al.* 1993), or basic behaviors such as nest defense activity (Ilmonen pers. comm.).

That subclinical disease can affect reproductive performance, life history strategies, and survival in wild bird populations is not surprising if one considers the large body of information available in the domestic poultry literature. In growing commercial poultry, subclinical disease, regardless of the etiologic agent, results in decreased growth rates, reduced feed consumption and feed conversion rates, retarded physiologic maturation leading to slow feathering patterns, and reduced immune competence etc., without causing overt clinical disease or mortality. Any of these sorts of physiologic changes induced by subclinical diseases in wild species must reduce the chances of juvenile survival. In adult breeder or commercial laying hens, the first indication of subclinical disease is a reduction or complete cessation of egg production. Parasites and most pathogens compete for critical resources and during periods resource decline, for example during a period of declining food availability, the host maintains itself at the expense of reproduction or offspring survival. This strategy makes sense in species with a relatively long reproductive life span.

In our Great Horned Owl study, black fly feeding, the effects of infection with *Leucocytozoon* spp., and likely other unrecognized subclinical disease occurrences all compete for host resources. We suspect that even in years when mortality due to parasitism is low, black fly feeding may influence other aspects of Great Horned Owl behavior such as nest site selection, timing of nesting, and roost site selection of fledglings. The recognition and biologic importance of subclinical disease has received little attention by researchers, yet may yield interesting and important biological information about the life history strategies of wild species.

LITERATURE CITED

Bennett, G.P.; Peirce, M.A.; Ashford, R.W. 1993. Avian haematozoa: mortality and pathogenicity. Journal of Natural History. 27: 993-1001.

Clayton, D.H. 1991. The influence of parasites on host sexual selection. Parasitology Today. 7: 329-334.

Currie, D.C. 1997. Black flies (Diptera: Simuliidae) of the Yukon, with reference to the black fly fauna of northwestern North America. In: Downes, J.A.; Danks, H.V., eds. Insects of the Yukon. Ottawa, Canada: Biological Survey of Canada (Terrestrial Arthropods). In press.

Edgar, S.A. 1953. A field study of the effect of black fly bites on egg production of laying hens. Poultry Science. 32: 779-780.

Fredeen, F.J.H. 1969. Outbreaks of the black fly *Simulium articum* (Malloch) in Alberta. Quaestiones Entomologicae. 5: 341-72.

Harwood, R.F.; James, M.T. 1979. Gnats, black flies, and related forms. In: Entomology in human and animal health, 7th ed. MacMillan Publishing Co.: 148-149.

Herman, C.M.; Barrow, J.H., Jr.; Tarshis, I.B. 1975. Leucocytozoonosis in Canada geese at the Seney National Wildlife Refuge. Journal of Wildlife Diseases. 11: 404-411.

Hudson, P.J.; Dobson, A.P.; Newborn, D. 1992. Do parasites make prey vulnerable to predation? Red grouse and parasites. Journal of Animal Ecology. 61: 681-692.

Hunter, D.B.; Rohner, C.; Currie, D.C. 1997. Black flies (Simuliidae) and blood parasites (Leucocytozoon spp.) as causes of mortality in fledgling Great Horned Owls. Journal of Wildlife Diseases (in press, vol.)

Korpimäki, E.; Hakkarainen, H.; Bennett, G.F. 1993. Blood parasites and reproductive success of Tengmalm's Owls: detrimental effects on females but not on males? Functional Ecology. 7: 420-426.

Peirce, M.A. 1981. Current knowledge of the haematozoa of raptors. In: Cooper, J.E.; Greenwood, A.G., eds. Recent advances in the study of raptor diseases. Keighley, West Yorkshire, England: Chiron Publications: 15-19.

Rohner, C.; Doyle, F.I. 1992. Methods of locating Great Horned Owl nests in the boreal forest. Journal of Raptor Research. 26: 33-35.

Rohner, C. 1994. The numerical response of Great Horned Owls to the snowshoe hare cycle in the boreal forest. Vancouver, BC: University of British Columbia. Ph.D. dissertation.

Rohner, C.; Hunter, D.B. 1996. First-year survival of Great Horned Owls during a peak and decline of the snowshoe hare cycle. Canadian Journal of Zoology. 74: 1092-1097.

Sutcliffe, J.F.; McIver, S.B. 1984. Mechanics of blood-feeding in black flies (Diptera: Simuliidae). Journal of Morphology. 180: 125-144.

Temple, S.A. 1987. Do predators always capture substandard individuals disproportionately from prey populations? Ecology. 68: 669-674.

Distribution, Abundance, and Habitat Use of Territorial Male Boreal Owls (*Aegolius funereus*) in Northeast Minnesota

William H. Lane, David E. Andersen, and Thomas H. Nicholls[1]

We conducted nocturnal auditory surveys from 1987-1992 to determine the distribution, abundance, and habitat use of Boreal Owls (*Aegolius funereus*) in northeast Minnesota. We concentrated our efforts in areas where documented nesting attempts by the owls had occurred, along roadways maintained for winter-time access by motor vehicles, and by traversing all habitat types found within the study area.

Survey efforts were generally initiated by 15 March each year and consisted of 3 min listening stations at 0.8 km intervals. Surveys were not conducted during moderate to heavy precipitation or in winds exceeding 23 km/ph. At each stop observers listened for the staccato song, the primary vocalization of the male Boreal Owl. When an owl was detected, a directional azimuth was recorded and the distance to the owl estimated qualitatively. Additional directional azimuths from subsequent listening stations were recorded to facilitate a more accurate placement of the owl's location.

Two owl abundance indices were derived from survey efforts, one based on all owl detections/ total km surveyed (representing the encounter rate), and one based on the cumulative number of individual owls located along the length of each survey route (an index of density). Owl detections were placed into one of two categories: Unique (new) detections were assigned to owls the first time they were detected within a given landscape, whereas owls heard within 1.8 km of an initial detection point during subsequent surveys were considered the same owl (repeat) unless there was evidence of more than one owl within a given location (i.e., simultaneous vocalizations).

To determine the habitat used by Boreal Owls during courtship activities, owl locations (derived from on-the-ground foot searches) were assigned forest stand characteristics according to USDI Geological Survey 1:24,000 topographic maps, aerial photographs, and USDA Forest Service compartment folder analysis. To determine the habitat available to owls along the survey routes, we first established an effective range of detection for vocalizing owls (i.e., 92 percent of vocalizing owls were heard from within 2.0 km of a survey point) and subsequently constructed a scaled 4 km^2 grid as the sampling basis for habitat evaluation. Habitat used and habitat available were categorized according to habitat type, stand size density, and acreage. The proportion of each habitat type and density was then tabulated for "used" versus "random" locations. Chi-square and Bonferroni Confidence Interval tests were conducted to determine if a difference existed between observed habitat use and expected use according to habitat availability.

RESULTS

From 1987 to 1992, singing male owls were detected on 234 occasions during 4,998.2 km of surveys, representing an overall encounter rate of 0.047 detections/km surveyed. The lowest annual encounter rate was recorded in 1991 (0.030 owls/km surveyed), and the highest in 1989 (0.089 owls/km surveyed). When the abundance of individual owls/route length were calculated, the lowest indices occurred in 1987 (0.059 owls/linear km), and the highest occurred in 1989 (0.219 owls/ linear km). Combined, the encounter rate and abundance index suggest a 3 year periodicity in owl numbers, with peaks recorded in 1989 and 1992, and lows in 1987 and 1990. Previously detected owls accounted for 63 (26.9 percent) of 234 detections, and were most prevalent during 1989 when 33 (37.5 percent) of eight Boreal Owls heard were categorized as previously detected. During 1988 and 1989, 90 (69.7 percent) of 129 Boreal Owls were located prior to 15 April. An analysis of singing activity suggested that encounter rates increased towards 15 April and gradually decreased thereafter.

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Owls were widely distributed throughout the study area, although differences in abundance were noted along portions of the survey routes. Specifically, sawtimber-sized stands (dominated by cavity-substrate trembling aspen (*Populus tremuloides*)) were used significantly more, and regenerative stands significantly less (both at $P = 0.05$) than expected by the owls for courtship activities, based on availability within the landscape.

Our results indicate that Boreal Owls occur as a regular breeding species at low densities, and that they select older aspen-dominated habitats for their nesting activities in northeast Minnesota. Although Boreal Owls are prone to annual population fluctuations, possibly due to prey availability and winter conditions, the current 40 year rotation emphasis on timber harvests in aspen dominated, upland-mixed type forests could negatively impact population size and distribution of Boreal Owls across the landscape of northeast Minnesota.

Habitat Use and Movements of Breeding Male Boreal Owls (*Aegolius funereus*) in Northeast Minnesota as Determined by Radio Telemetry

William H. Lane, David E. Andersen, and Thomas H. Nicholls[1]

To determine habitat use and movements of male Boreal Owls (*Aegolius funereus*) in northeast Minnesota, we monitored 10 radio-equipped owls from 1990-1992. We used mist nets, bal-chartris, and the taped playback recording of the primary song of the male Boreal Owl to trap territorial male owls during the springtime breeding season. Owls were outfitted with 5.2 g backpack-type transmitters and monitored using a scanning receiver and a hand held, three-element Yagi antenna. Initial diurnal locations were estimated from directional azimuths obtained from landmark locations, followed by walk-ins to the roost site. At each roost site, a series of qualitative and quantitative habitat descriptions was recorded from within a 0.04 ha circular plot, centered on the roost tree. Roost site locations were recorded on aerial photographs and converted to Universal Transverse Mercator (UTM) coordinates. Nocturnal movement patterns were assessed, based on synchronous telemetry readings by at least two observers from predetermined locations. Observers recorded directional azimuths to the owl from a varying number of relocations with a minimum of 10 min separating successive relocation efforts.

A Minimum Convex Polygon (MCP) was generated to describe the boundary within which owl movements were recorded, and a 50 percent Harmonic Mean Transformation-Activity Area (HMT-AA) was used to depict areas of concentrated use. To evaluate the habitat used by nesting Boreal Owls, we drew MCP boundaries (based on roost site locations) atop USDA Forest Service compartment maps (1:15,480) and extracted stand data from within the perimeter of the MCP. Habitat available to owls was determined by pooling random habitat samples from call-survey routes located adjacent to MCP locations. Both the habitat used and habitat available to owls were classified according to forest type, stand density, and areal extent.

RESULTS

Of the 10 radio-tagged owls, six presumably left the study area, one was killed by an avian predator, and three remained in the study area throughout the monitoring period (mid-June of each year). One owl, radio-tagged during its 1991 nesting season, was retrapped in 1992, less than 1 km from its 1991 nest site. Boreal Owls typically roosted in lowland areas characterized by thick, homogeneous coniferous growth. Black spruce (*Picea mariana*) was used as the roost tree at 94 (81.7 percent), balsam fir (*Abies balsamea*) at 10 (8.7 percent), and northern white-cedar (*Thuja occidentalis*) at 5 (4.3 percent) of 115 observed roost sites.

The average MCP home range estimate for nesting male Boreal Owls was 1,202 ha ($n = 4$; range = 742-1,444 ha). However, MCP size appeared to be influenced by owl movements following nesting attempts. Analysis of 50 percent HMT-AA estimates suggested that owls concentrated their activities within relatively small areas in comparison to MCP home range size.

Habitat composition within home range perimeters varied considerably from random habitat samples taken from adjacent call-survey routes. Rank tests for habitat usage and availability suggest that lowland conifers were the most preferred and upland mixed-type forests the least preferred habitat features used for roosting within the landscape.

Our results indicate that Boreal Owls use a diversity of habitat types for nesting and non-nesting activities in northeast Minnesota. Specifically, based on nest site locations and locations of singing male owls, Boreal Owls are associated with mature, upland, mixed-type

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forests for nesting activities. Lowland homogeneous conifer forests are preferred for roosting and foraging activities. Although Boreal Owls are prone to annual population fluctuations, due to prey availability and winter conditions, factors that negatively affect landscape scale features identified by our study as important to owls, will likely affect both long term population size and distribution of Boreal Owls in northeast Minnesota.

Territories of Flammulated Owls (*Otus flammeolus*): Is Occupancy a Measure of Habitat Quality?

Brian D. Linkhart and Richard T. Reynolds[1]

Abstract.—Annual territory occupancy by Flammulated Owls (*Otus flammeolus*) in Colorado was evaluated from 1981-1996. Fourteen territories occurred within a 452 ha study area. Each year, three to six territories were occupied by breeding pairs and three to seven were occupied by unpaired males. Territories were occupied by breeding pairs a mean of 5.1 years (not necessarily consecutive) and by unpaired males a mean of 3.9 years (not necessarily consecutive). Territories most consistently occupied by breeding pairs contained the highest percentage of old (200-400 years) ponderosa pine/ Douglas-fir, whereas territories least occupied by breeding pairs contained the least amount of this vegetation type.

Little is known about habitat selection in the Flammulated Owl (*Otus flammeolus*), an insectivorous and migratory species (Balda *et al.* 1975, Phillips 1942, Ross 1969). The owl is an obligate cavity-nester (Earhart and Johnson 1970) and commonly breeds in ponderosa pine (*Pinus ponderosa*), Jeffrey pine (*P. jeffreyi*), and mixed-conifer forests of western North America (Cannings *et al.* 1978; Reynolds and Linkhart 1984, 1987; Sutton and Burleigh 1940; Winter 1974).

A model proposed by Fretwell and Lucas (1970) suggested that in stable, heterogeneous environments, birds first settle into high-quality habitats (i.e., habitats in which birds have the highest reproductive success) until these habitats are saturated, then settle into habitats of poorer quality where reproduction may be lower. We examined this model of habitat selection by associating habitat conditions in territories with the extent to which territories were occupied by Flammulated Owls. Our hypothesis is that territories occupied by breeding pairs every year are the highest quality, and the poorer-quality territories are occupied only occasionally by breeding adults. We have assumed that over the study the relative quality of territories changed little, and territory boundaries remained relatively stable. Here we rank 14 territories on the number of years each was occupied by breeding owls, and describe differences in forest overstories within territories according to the ranking.

STUDY AREA

The 452 ha study area was located in central Colorado on the Manitou Experimental Forest, Teller County. Boundaries of the study area were established during initial surveys in 1980 to include approximately 15 to 20 territorial Flammulated Owls. Forests within the study area consisted of (1) ponderosa pine mixed with Douglas-fir (*Pseudotsuga menziesii*), generally on ridgetops and south- and west-facing slopes; (2) quaking aspen (*Populus tremuloides*) stands, on the bottoms and lower slopes of moist drainages; (3) quaking aspen stands mixed with blue spruce (*Picea pungens*), in bottoms, lower slopes, and benches in moist areas; and (4) Douglas-fir mixed with blue spruce, at higher elevations and on north-facing slopes. Tree cutting on the study area had not occurred since the 1880's, when a light harvest for railroad ties occurred. There were a mean of 1.3 snags and live trees with cavities per hectare in the study area (Reynolds *et al.* 1985). The study area was surrounded by forests composed of a similar mix of forest types and ages.

METHODS

The study was conducted from May to September, 1981-1996. Each spring and summer, we searched the entire study area for territorial males (Marshall 1939). Territories were identified by marking territorial song-trees of males (Reynolds and Linkhart 1984), and by using radio-telemetry during 1982-1983 (Linkhart 1984). Once territory boundaries were delineated, we located all suitable nesting cavities (tree cavities with entrance diameters >4 cm) within territories and checked each for nesting owls (Reynolds and Linkhart 1984). Adults were captured at nests (occasionally on perches or day roosts) and banded with U.S. Fish and Wildlife Service leg bands (Reynolds and Linkhart 1984). Non-nesting owls were not usually captured. Each year, we determined the breeding status of all territorial males by searching for nests and monitoring the owls' behavior. Unpaired males typically sang throughout the breeding season, whereas singing in breeding males dramatically declined after the pairs' eggs hatched (Reynolds and Linkhart 1987). A total of 69 adults (32 males and 37 females) were banded on the study area in the 16 years.

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Four forest types, distinguished by plurality of tree species and age (determined with increment borer) of overstory, occurred in the study area: old (200-400 years) ponderosa pine/ Douglas-fir; mature (100-200 years) quaking aspen/blue spruce; mature (75-125 years) quaking aspen; and young (<100 years) Douglas-fir/blue spruce. A meadow (grass/ forbs) vegetation type was also identified on the study area. Areas of each type greater than 0.1 ha were delineated on aerial photographs (scale 1:1,000) of the study area. A circle with radius of 212 m (mean radius for territories of Flammulated Owls delineated by radio-telemetry (Linkhart 1984) was inscribed on aerial photographs corresponding to the area defended by each territorial male. The percent area occupied by vegetation types in each "habitat circle" was determined by overlaying an acetate grid (2 x 2 mm = 10 x 10 m ground-equivalent, 660 total grid squares) on the inscribed circle and counting the number of squares fully occupied by each vegetation type. Portions (20-50 percent) of habitat circles for four territories (A2, A7, A13, and A20) extended beyond the bounds of the study area; for these habitat circles, we calculated percentages of vegetation types that occurred only within the study area (vegetation types were not delineated outside of the study area). One territory (A40) was excluded from analysis because its occupancy status was only determined in 1995 and 1996.

We determined the occupancy status (breeding pair, unpaired male, or unoccupied) of all territories each year from 1981-1996. Frequency of occupancy status was compared among territories using a contingency table. We used Spearman rank correlation (Snedecor and Cochran 1967) to determine if the number of years territories were occupied by breeding pairs was correlated with the percent of vegetation types within habitat circles. The null hypothesis was no correlation of occupancy with vegetation types. For all tests, results were significant if $P < 0.05$.

RESULTS

Fourteen territories occurred on the study area from 1981-1996 and each was occupied by breeding pairs and unpaired males a mean of 8.9 years (SD = 4.6, range = 3-16 years) (years not necessarily consecutive) (table 1). Each year three to six territories were occupied by breeding pairs and three to seven territories were occupied by unpaired males. Most territories remained relatively fixed in space over the 16 year study, with two notable exceptions. The A24 territory was only occupied from 1981-1983. In 1984, the male in an adjacent territory (A29) expanded his movements and activities into much of the area formerly in A24 territory. A portion of A15 territory, only occupied from 1981-1984, was incorporated in the same manner in 1985 by the A8 male.

Territories were occupied by breeding pairs a mean of 5.1 years (SD = 4.1, range = 0-14 years) (years not necessarily consecutive) (table 1). Rate and type of occupancy differed among territories ($X^2 = 95.6$, d.f. = 22, $P < 0.001$). Two territories (A4 and A29) were occupied by breeding pairs for 12 or more years, while eight territories (A12, A7, A15, A24, A18, A27, A20, and A2) were occupied by breeding pairs for 4 or fewer years (table 1). Territories were occupied by unpaired males a mean 3.9 years (SD = 3.0, range = 0-10 years) (years not necessarily consecutive) (table 1). Two territories (A12 and A18) were occupied by unpaired males 9 or more years and two (A15 and A24) were never occupied by unpaired males (table 1). Six territories (A12, A7, A18, A27, A20, and A2) were occupied more often by unpaired males than breeding pairs (table 1).

Territories occurred throughout the study area and the mean percent vegetation composition

Table 1.—*Number of years territories were occupied by Flammulated Owls (*Otus flammeolus*) in Colorado, 1981-1996.*

Territory	Number of years occupied by Breeding pairs	Number of years occupied by Unpaired males	Total years occupied
A4	14	1	15
A29	12	4	16
A8	7	6	13
A11	7	4	11
A13	7	2	9
A10	6	3	9
A12	4	9	13
A7	3	5	8
A15[1]	3	0	3
A24[2]	3	0	3
A18	2	10	12
A27	2	5	7
A20	1	2	3
A2	0	3	3
MEAN	5.1	3.9	8.9
SD	4.1	3.0	4.6

[1] Not occupied after 1984 when A8 male expanded his territory into portions of A15.

[2] Not occupied after 1983 when A29 male expanded his territory into most of A24.

within habitat circles was similar to the percent vegetation composition of the entire study area (table 2). Thus, Flammulated Owls appeared to use all available habitats within the study area (sensu Fretwell and Lucas 1970). However, individual habitat circles contained from 27 to 94 percent old ponderosa pine/Douglas-fir. Four habitat circles (A4, A15, A24, and A29) contained more than 75 percent old ponderosa pine/Douglas-fir, while five habitat circles (A12, A18, A27, A20, and A2) contained less than 50 percent of this type (table 2). Habitat circles also contained from 0 to 65 percent young Douglas-fir/blue spruce, and four habitat circles (A12, A18, A20, and A2) contained more than 45 percent of this type, while eight habitat circles (A4, A29, A8, A11, A10, A7, A15, and A24) contained less than 10 percent (table 2).

Occupancy of territories by breeding pairs was positively correlated with the amount of old ponderosa pine/Douglas-fir in habitat circles ($r_s = 0.75$, $P < 0.01$, $n = 12$), and was negatively correlated with the amount of young Douglas-fir/blue spruce in habitat circles ($r_s = -0.72$, $P < 0.01$, $n = 12$) (A15 and A24 were omitted from the rank correlation, since these territories were subsumed by males in adjacent territories). Thus, territories most frequently occupied by breeding pairs had habitat circles containing the highest percentages of old ponderosa pine/Douglas-fir and the least percentages of young Douglas-fir/blue spruce. Occupancy of territories by breeding pairs was not correlated with mature blue spruce/quaking aspen ($r_s = -0.04$, $P = 0.90$, $n = 12$), mature quaking aspen $r_s = 0.49$, $P = 0.11$, $n = 12$), or meadow ($r_s = 0.45$, $P = 0.20$, $n = 12$), in habitat circles.

DISCUSSION

We distinguished three categories of years that breeding pairs occupied territories: (1) 12 or more years, (2) 6 and 7 years, and (3) 4 or fewer years. Territories occupied 12 or more years (A4 and A29) had habitat circles containing more than 75 percent old ponderosa pine/Douglas-fir, with less than 13 percent of any other vegetation type. Territories occupied for 6 and 7 years (A8, A11, A13, and A10) had habitat circles containing 54-74 percent old ponderosa pine/Douglas-fir, with up to 35 percent of the other vegetation types. Territories most often occupied by unpaired males and rarely by breeding pairs (A12, A7, A18, A27, A20, and A2) had habitat circles containing 27 to 68 percent old ponderosa pine/Douglas-fir, with up to 65 percent of the other vegetation types. Two territories, A15 and A24, were occupied for only 3 years by breeding pairs and had habitat circles containing more than 78 percent old ponderosa pine/Douglas-fir. However, portions of these territories were taken over by adjacent territorial males (A8 and A29, respectively) in 1984 (A24) and 1985 (A15).

Territories that were occupied by breeding pairs most of the 16 years also produced the most owlets (> 16 total young, unpubl. data) over the study. These territories likely confer the greatest fitness to individuals and may act as sources of owls to occupy other habitats (sensu Pulliam 1988). Territories that were most often occupied by non-breeding owls produced the fewest owlets (< 8, unpubl. data), and may act as sinks for the population (sensu Pulliam 1988).

Our long-term data suggests that territory occupancy may be an indicator of habitat quality for Flammulated Owls. Old ponderosa

Table 2.—*Percent vegetation composition in Flammulated Owl (*Otus flammeolus*) habitat circles in Colorado, ranked by number of years territories were occupied by breeding pairs, 1981-1996.*

Territory	Old (200-400 yr) ponderosa pine/ Douglas-fir	Young (<100 yr) Douglas-fir/ blue spruce	Mature (100-200 yr) blue spruce/ quaking aspen	Mature (75-125 yr) quaking aspen	Meadow
A4	94	0	0	6	0
A29	76	3	12	6	3
A8	72	7	0	16	5
A11	55	6	33	6	0
A13[1]	54	35	11	0	0
A10	74	5	21	0	0
A12	32	46	18	4	0
A7[1]	68	0	0	32	0
A15[2]	87	7	0	6	0
A24[3]	79	2	8	11	0
A18	27	65	8	0	0
A27	42	41	17	0	0
A20[1]	36	51	12	1	0
A2[1]	49	47	4	0	0
Mean	60	23	10	6	1
SD	21	23	10	9	2
Study Area	58	27	11	3	1

[1] Percent overstory in habitat circles (see text) presented only for the proportion of circles occurring within the study area.

[2] Not occupied after 1984 when A8 male expanded his territory into portions of A15.

[3] Not occupied after 1983 when A29 male expanded his territory into most of A24.

pine/Douglas-fir appears to be the best breeding habitat for the owls; territories most consistently occupied by breeding pairs had habitat circles containing the highest percentage of this vegetation type, while territories least occupied by breeding pairs had habitat circles containing the least amount of this vegetation type. Breeding by owls occurred less often in territories where habitat circles contained higher percentages of young Douglas-fir/blue spruce. Other vegetation types (mature blue spruce/quaking aspen, mature quaking aspen, and meadow) occurring in habitat circles were not correlated with the number of years territories were occupied by breeding pairs. The extent to which territory occupancy is an indicator of habitat quality in Flammulated Owls requires corroboration by correlating habitat structure and floristics with other demographic parameters, such as reproduction, survival, tenure, and fidelity of owls on territories.

A correlation between territory occupancy and territory quality was found in other birds. Territories most often occupied by breeding pairs contained the highest-quality habitats in black-billed Magpies (*Pica pica*) (Baeyens 1981), Bobolinks (*Dolichonyx oryzivorus*) (Bollinger and Gavin 1989), Tengmalm's Owl (*Aegolius funereus*) (Korpimäki 1988), and European Sparrow-hawks (*Accipiter nisus*) (Newton and Marquiss 1976, 1982).

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LITERATURE CITED

Baeyens, G. 1981. Functional aspects of serial monogamy: the Magpie pair-bond in relation to its territorial system. Ardea. 69: 145-166.

Balda, R.P.; McKnight, B.C.; Johnson, C.D. 1975. Flammulated Owl migration in the southwestern United States. Wilson Bulletin. 87: 520-532.

Bollinger, E.K.; Gavin, T.A. 1989. The effects of site quality on breeding-site fidelity in Bobolinks. Auk. 106: 584-594.

Cannings, R.J.; Cannings, S.R.; Cannings, J.M.; Sirk, G.P. 1978. Successful breeding of the Flammulated Owl in British Columbia. Murrelet. 59: 74-75.

Earhart, C.M.; Johnson, N.K. 1970. Size, dimorphism, and food habits of North American owls. Condor. 72: 251-264.

Fretwell, S.; Lucas, H. 1970. On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheoretica. 19: 16-52.

Korpimäki, E. 1988. Effects of territory quality on occupancy, breeding performance, and breeding dispersal in Tengmalm's Owl. Journal of Animal Ecology. 57: 97-108.

Linkhart, B.D. 1984. Range, activity, and habitat use by nesting Flammulated Owls in a Colorado ponderosa pine forest. Fort Collins, CO: Colorado State University. 45 p. M.S. thesis.

Marshall, J.T., Jr. 1939. Territorial behavior of the Flammulated Screech Owl. Condor. 41: 71-78.

Newton, I.; Marquiss, M. 1976. Occupancy and success of nesting territories in the European Sparrowhawk. Journal of Raptor Research. 10: 65-71.

Newton, I.; Marquiss, M. 1982. Fidelity to breeding area and mate in Sparrowhawks *Accipiter nisus*. Journal of Animal Ecology. 51: 327-341.

Phillips, A.R. 1942. Notes on the migrations of the Elf and Flammulated Screech Owls. Wilson Bulletin. 54: 132-137.

Pulliam, H.R. 1988. Sources, sinks, and population regulation. American Naturalist. 132: 652-661.

Reynolds, R.T.; Linkhart, B.D. 1984. Methods and materials for capturing and monitoring Flammulated Owls. Great Basin Natural. 44: 49-51.

Reynolds, R.T.; Linkhart, B.D. 1987. The nesting biology of Flammulated Owls in Colorado. In: Nero, R.W.; Clark, R.J.; Knapton, R.J.; Hamre, R.H., eds. Biology and conservation of northern forest owls: symposium proceedings; 1987 February 3-7; Winnipeg, MB. Gen. Tech. Rep. RM-142. Fort Collins, CO: U.S. Depart-ment of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 239-248.

Reynolds, R.T.; Linkhart, B.D.; Jeanson, J. 1985. Characteristics of snags and trees containing cavities in a Colorado conifer forest. Res. Note RM-455. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 6 p.

Ross, A. 1969. Ecological aspects of the food habits of insectivorous Screech Owls. Proceedings of the Western Foundation of Vertebrate Zoology. 1: 301-344.

Snedecor, G.W.; Cochran, W.G. 1967. Statistical methods. Ames, IA: The Iowa State University Press. 593 p.

Sutton, G.M.; Burleigh, T.D. 1940. Birds of Las Vigas, Vera Cruz. Auk. 57: 234-243.

Winter, J. 1974. The distribution of the Flammulated Owl in California. Western Birds. 5: 25-43.

Metapopulation Dynamics of a Burrowing Owl (*Speotyto cunicularia*) Population in Colorado

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Abstract.—We banded 555 Burrowing Owls (*Speotyto cunicularia*) either as adults (after hatch year; AHY) or as young of the year (hatch year; HY) and used capture-recapture models to estimate survival and recapture rates and Leslie matrix models to project population growth over time at the 6,900-ha Rocky Mountain Arsenal National Wildlife Refuge (RMANWR), Colorado from 1990-1994. We found survival rates for AHY could be pooled across sexes and that survival varied by year. Survival for AHY birds between 1990-1991 was 0.71 and averaged 0.18 for the period 1991-1994 ($P = 0.06$). Survival for HY birds was lower (0.12) the first year of life than succeeding years ($\bar{x} = 0.62$, $P = 0.0006$). We modeled populations on the Refuge as a combination of birds using 'good' and one of two types of 'fair' habitats. In all models, the proportion of birds that used the good habitat was not critical to population persistence. Our models suggest that RMANWR could act as a source if the population used the combination of good and an 'increasing' fair habitat. Our model also suggests that number of pairs using RMANWR decline (5-20 percent) when we used good habitat combined with 'average' fair habitat.

Burrowing Owls (*Speotyto cunicularia*) are a species of concern throughout much of their range in the United States (Rich 1984) and Canada (Ratcliff 1986, Johnsgard 1988). Eradication of burrowing mammals that provide nest sites for Burrowing Owls (Butts 1973, Zarn 1974) and habitat loss to development by humans (Zarn 1974) are principal factors suspected in owl population declines. In Colorado, migratory Burrowing Owls depend chiefly on black-tailed prairie dogs (*Cynomys ludovicianus*) for nesting burrows, and often return to nesting areas used previously (Plumpton and Lutz 1993b). Philopatry by marked Burrowing Owls (Martin 1973), and nest site fidelity by populations (Gleason 1978, Rich 1984) have been identified as traits of Burrowing Owls.

We investigated survival and reproductive performance in a migratory population of Burrowing Owls. Our objectives were to determine: (1) age class and gender-specific survival rates and; (2) to model population trajectories using our estimates of these vital statistics.

MATERIALS AND METHODS

Study Area

We studied Burrowing Owls on the Rocky Mountain Arsenal National Wildlife Refuge (RMANWR) 16 km from Denver, Colorado, in southwestern Adams County. This 6,900-ha area is vegetated primarily by weedy forbs, cheatgrass (*Bromus tectorum*), and perennial grasses. Shrubs include yucca (*Yucca* spp.), sand sagebrush (*Artemisia filifolia*), and rubber rabbitbrush (*Chrysothamnus nauseosus*) that occur in patches throughout the area. Cottonwood (*Populus sargentii*) and willow (*Salix* spp.) occur along riparian areas and where planted. Black-tailed prairie dog colonies were present throughout the area, and provided the sole nesting habitat of Burrowing Owls.

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Capture And Banding

We captured and banded Burrowing Owls during the breeding seasons (1 April - 31 July) from 1990-1994. We used primarily Sherman and Tomahawk traps to capture nesting Burrowing Owls and their young (Plumpton and Lutz 1992, 1993a). We banded owls with visual identification (VID) color-anodized aluminum legbands engraved with unique alpha/numeric combinations (Acraft Sign and Nameplate Co., Ltd., Edmonton, Alberta, Canada) and classified owls as either hatch year (HY) or adult (after hatch year; AHY) based on size and plumage. We surveyed the study site daily during the breeding season to locate nest burrows, count young, and trap owls. Our surveys consisted of driving roads and using spotting scopes mounted on vehicle windows to identify nesting and previously banded Burrowing Owls. We also traversed prairie dog towns on foot, inspecting burrows for signs of occupancy by Burrowing Owls (whitewash, castings, and prey remains). We defined mated pairs as those that used a single burrow and attempted to nest, and successful nesting attempts as those where ≥1 young was fledged (Steenhof 1987). We estimated brood size as the maximum number of young seen at each burrow prior to fledging.

Survival

We used capture-recapture models and methods (Burnham and Anderson 1992, Lebreton *et al.* 1992) to estimate survival (Φ) and recapture (*p*) probabilities. We followed notation of Lebreton *et al.* (1992). In our most general model for AHY owls, we varied survival and recapture probabilities by time (*t*), sex (*s*), and/or age (*a*). For HY birds, we varied Φ and *p* by *t* and/or *a*. We used goodness-of-fit tests in RELEASE (Burnham *et al.* 1987) to evaluate pooling across groups (e.g., *t, a, s*) for further analyses and SURGE 4.1 (Pradel *et al.* 1990) for model building. We used Akaike's Information Criterion (AIC) (Burnham and Anderson 1992) to select parsimonious models, and likelihood-ratio tests (LRT) to determine significance between general and reduced models. We tested the hypotheses that group survival rates within AHY and HY were similar using chi-square tests (Sauer and Williams 1989). Our survival rates should be interpreted as apparent survival rates because we have no estimate of dispersal in this population.

Model

We used a stage-structured Leslie matrix (Leslie 1945) where the first two stages corresponded to annual age classes to project population growth for a population of 35 pairs over 50 years. We modeled demographic parameters using a normal distribution to account for stochasticity. We investigated the influence of habitat quality on population trajectories by modeling population growth in two types of habitat, good and fair. We used maximum values for our parameters to describe the dynamics in the good habitat. We defined fair habitat in two different ways. In one approach, we used average values for our parameters. We refer to this as 'average' fair conditions. In another approach to fair habitat, we manipulated AHY survival (within the range of our estimates) until we generated a lambda of > 1.0. We refer to this as 'increasing' fair conditions. Additionally, we modeled population trajectories when 2 percent and 33 percent of individuals in the population occupied good habitat.

RESULTS AND DISCUSSION

We banded 555 Burrowing Owls (table 1); this provided 4 consecutive years of potential return to RMANWR (1991-1994) involving 514 individuals (those banded before 1994). During all nesting years (1990-1994), 202 of 334 nesting adults (60 percent) were known individuals. We estimate that this population fledged 585 owlets from 1990-1993; we banded 369 (63 percent) of these owlets.

Survival

We did not have sufficient data to use goodness-of-fit tests in RELEASE; we did build reduced models in SURGE. Adult male and female survival and recapture rates did not vary (survival: $X^2 = 3.978$, 2 *df*, $P = 0.137$, recapture: $X^2 = 2.887$, 2 *df*, $P = 0.236$), so we pooled the sexes for analyses (table 1) and modeling. Our most reduced model for AHY revealed that adult survival was high in 1991 (71 percent) and averaged 18 percent in subsequent years ($X^2 = 3.4$, 1 *df*, $P = 0.06$). We found annual survival for owls banded during HY varied by age. For owls banded during HY, survival the first year of life average 12 percent and then increased to an average of 62 percent for the remaining years ($X^2 = 11.79$, 1 *df*, $P = 0.0006$).

Table 1.—*Estimates of annual survival (Φ) and recapture (p) probabilities for Burrowing Owls captured at Rocky Mountain Arsenal National Wildlife Refuge, Colorado, 1990-1994.*

Age[1]	Model[2]	Group[3]	Φ	SE[4]	p	SE
AHY	$(\Phi_{t'}, p)$	1990-1991	0.71	0.28	0.49	0.19
		1991-1994	0.18	0.06	0.49	0.19
HY	(Φ_{2a}, p)	age, 1-2 yr	0.12	0.04	0.35	0.13
		age, >2 yr	0.62	0.14	0.35	0.13

[1] Age at banding was either after hatch year (AHY) or hatch year (HY).

[2] We present estimates from the reduced models produced in SURGE.

[3] Group parameters were either time, 1990-1994, or age since capture.

[4] Standard Error.

Model

We used weighted averages to estimate AHY survival (0.37) and used 0.12 as an estimate of survival for HY birds. When we used these estimates of survival and an average of 3.5 fledglings/pair, this population had lambda of 0.79. When we used an average fecundity of 3.5 and 0.12 for HY survival, we found that AHY survival of 0.59 was the lower limit to maintain a population with lambda > 1.0. This estimate of AHY survival was within the range of our estimates, 0.18-0.71.

Some pairs were very successful at rearing young. We saw females return to the same nest site to breed after they had fledged an average of 4.2 young. We incorporated this phenomenon into our model by using this rate to describe fecundity in 'good' habitat. We defined the other parameters in good habitat as HY survival of 0.12, and AHY survival of 0.71 (maximum) to yield a lambda of 1.21. We defined fair habitat in two ways: (a) 'average'-fecundity of 3.5, HY survival of 0.12, AHY survival of 0.37 which resulted in a lambda of 0.79 or (b) 'increasing'-fecundity of 3.5, HY survival of 0.37, AHY survival of 0.59 which resulted in a lambda of 1.01.

In all combinations of good and fair habitat, we found population persistence (fig. 1). Our models resulted in RMANWR acting as a source population (Pulliam 1988) when we used combinations of good and 'increasing' fair habitat and indicated a decline over the 50 year time period when we modeled populations using good and 'average' fair habitat. The decline from year 1 to year 50 was approximately 20 percent when 2 percent of the population used the good habitat and 5 percent when 33 percent of the population used the good habitat.

We suggest that biologists continue to mark individuals so that demographic parameters can be better estimated. For this marking program to be useful, biologists must mark a high proportion of the population and trap each year so that enough owls are recaptured to reliably estimate survival rates. We urge biologists to continue to explore the relationships between owl social factors and productivity (Plumpton and Lutz 1994) and the relationships between burrowing owl productivity and prairie dog abundance and density (Plumpton and Lutz 1993b).

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LITERATURE CITED

Burnham, K.P.; Anderson, D.R. 1992. Data-based selection of an appropriate biological model: the key to modern analyses. In: McCullough, D.R.; Barrett, R.H., eds.

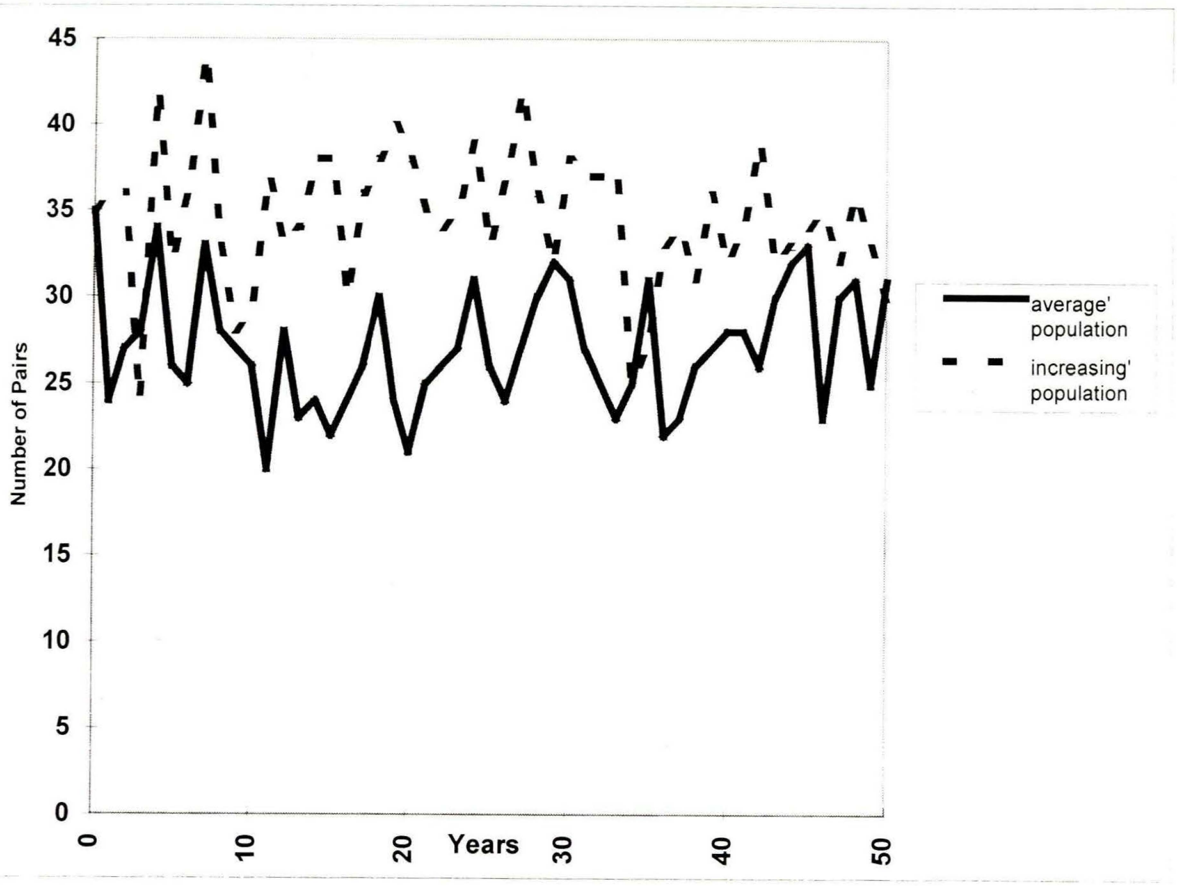

Figure 1.—*Burrowing Owl* (Speotyto cunicularia) *population projections using two types of fair habitat, increasing and average at Rocky Mountain Arsenal National Wildlife Refuge, Colorado.*

Wildlife 2001: populations. New York, NY: Elsevier Applied Science: 16-30.

Burnham, K.P.; Anderson, D.R.; White, G.C.; Brownie, C.; Pollock, K.H. 1987. Design and analysis methods for fish survival experiments based on release-recapture. American Fisheries Society Monograph 5. 437 p.

Butts, K.O. 1973. Life history and habitat requirements of Burrowing Owls in western Oklahoma. Stillwater, OK: Oklahoma State University. 188 p. M.S. thesis.

Gleason, R.S. 1978. Aspects of the breeding biology of Burrowing Owls in southeastern Idaho. Moscow, ID: University of Idaho. 47 p. M.S. thesis.

Johnsgard, P.A. 1988. North American owls: biology and natural history. Washington, DC: Smithsonian Institution Press: 170-177.

Lebreton, J-D.; Burnham, K.P.; Clobert, J.; Anderson, D.R. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs. 62: 67-118.

Leslie, P.H. 1945. On the use of matrices in certain population mathematics. Biometrika. 33: 183-212.

Martin, D.J. 1973. Selected aspects of Burrowing Owl ecology and behavior. Condor. 75: 446-456.

Pulliam, H.R. 1988. Sources, sinks, and population regulation. American Naturalist. 132: 652-661.

Plumpton, D.L.; Lutz, R.S. 1992. Multiple-capture techniques for Burrowing Owls. Wildlife Society Bulletin. 20: 426-428.

Plumpton, D.L.; Lutz, R.S. 1993a. Influence of vehicular traffic on time budgets of nesting Burrowing Owls. Journal of Wildlife Management. 57: 612-616.

Plumpton, D.L.; Lutz, R.S. 1993b. Nesting habitat use by Burrowing Owls in Colorado. Journal of Raptor Research. 27: 175-179.

Plumpton, D.L.; Lutz, R.S. 1994. Sexual size dimorphism, mate choice, and productivity of Burrowing Owls. Auk. 111: 724-727.

Pradel, R.; Clobert, J.; Lebreton, J-D. 1990. Recent developments for the analysis of capture-recapture multiple data sets. The Ring. 13: 193-204.

Ratcliff, B.D. 1986. The Manitoba Burrowing Owl survey 1982-1984. Blue Jay. 44: 31-37.

Rich, T. 1984. Monitoring Burrowing Owl populations: implications of burrow re-use. Wildlife Society Bulletin. 12: 178-180.

Sauer, J.R.; Williams, B.K. 1989. Generalized procedures for testing hypotheses about survival or recovery rates. Journal of Wildlife Management. 53: 137-142.

Steenhof, K. 1987. Assessing raptor reproductive success and productivity. In: Pendleton, B.A.G.; Millsap, B.A.; Cline, K.W.; Bird, D.M., eds. Raptor management techniques manual. Washington, DC: National Wildlife Federation: 157-170.

Zarn, M. 1974. Burrowing Owl (*Speotyto cunicularia hypugea*). Habitat management series for unique or endangered species. Tech. Note 242. Denver, CO: U.S. Bureau of Land Management. 25 p.

Is the Northern Saw-whet Owl (*Aegolius acadicus*) Nomadic?

Jeffrey S. Marks[1]

Expanded Abstract.—The first recorded nesting of a Northern Saw-whet Owl (*Aegolius acadicus*) in the Snake River Birds of Prey Area in southwestern Idaho occurred in a nest box in 1986. Occupancy of nest boxes by Northern Saw-whet Owls varied considerably (0 to 8 nests per year) over the next 10 years. Numbers of rodents fluctuated during this same period, and the number of nesting Saw-whets was positively correlated with an index of rodent abundance. In contrast, the number of nesting Western Screech-owls (*Otus kennicottii*) in the boxes was not significantly correlated with the rodent index. Moreover, numbers of nesting Saw-whets and Screech-owls were significantly positively correlated, indicating that the presence of Screech-owls in the boxes did not have a negative influence on the number of nesting Saw-whets each year.

Only one of the 46 breeding adult Saw-whets (a female) captured between 1987 and 1995 was recaptured in the study area in a subsequent year, and none of the 120 nestlings produced in the boxes has been re-encountered. A breeding male captured in April 1990 was found freshly dead in southern British Columbia in January 1993, approximately 900 km NNW of the study area. Data from the Bird Banding Laboratory are insufficient to evaluate breeding-site fidelity in Saw-whets because few researchers are banding Saw-whets at nests and because the records scheme is not designed for reporting captures of birds banded as breeders. Data from other studies of Saw-whets indicate that breeding-site fidelity is uncommon, and that patterns of nest-box occupancy vary geographically. Evidence from adult Saw-whets captured during fall migration suggests that birds tend to use the same migratory pathways from year to year. However, the data also are consistent with the hypothesis that if Saw-whets are nomadic, then the displacement of breeding areas is latitudinal rather than longitudinal.

Northern Saw-whet Owls exhibit most of the characteristics associated with nomadism in birds (i.e., high fecundity and use of scarce nest sites). I suggest that in some parts of their range, Saw-whets are nomadic, settling to breed in areas of high food availability (and, presumably, adequate nest-site availability) that they encounter during the winter. Among owls, nomadism is best documented in Boreal [Tengmalm's] Owls (*Aegolius funereus*) that feed on voles that undergo population cycles. Unlike Boreal Owls, Northern Saw-whet Owls feed mainly on *Peromyscus*, whose numbers are not known to vary in a predictable fashion. My conclusions are tentative because the amount of suitable data on nesting Saw-whets is pitifully small. An obvious need exists for studies of Northern Saw-whet Owls in which all adults and nestlings are banded each year and in which an index of food abundance is available.

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A 20-year Study of Barn Owl (*Tyto alba*) Reproduction in Northern Utah

Carl D. Marti[1]

Expanded Abstract.—I studied reproduction of the Barn Owl (*Tyto alba*) in northern Utah from 1977 through 1996 documenting 451 nesting attempts by at least 500 individuals. The study site was a narrow valley bounded by the Wasatch Mountains and the Great Salt Lake. This area was formerly shrubsteppe desert, but that community is now entirely supplanted by irrigated agriculture and urban development. Hot dry summers and cold winters characterize the region; mean temperatures for July and January are 23.9°C and -3.5°C. No natural nest sites suitable for Barn Owls exist on the area, and all Barn Owls nested in artificial structures, mostly nest boxes. Winter weather had a strong influence on the population's reproduction. Persistent snow cover and cold temperatures significantly delayed onsets of egg laying and reduced the number and success of breeding attempts. Clutch size, however, did not differ significantly among years or among nest sites. Complete first clutches averaged 7.25 eggs (n = 360). Replacement ($\bar{x}$ = 5.63, n = 19) and second clutches ($\bar{x}$ = 5.69, n = 39) were significantly smaller than first clutches, but replacement and second clutches were not significantly different. Sizes of first ($\bar{x}$ = 5.51, n = 314) and second broods ($\bar{x}$ = 5.69, n = 32) did not differ significantly, but replacement broods ($\bar{x}$ = 4.00, n = 12) were significantly smaller than both first and second broods. Of all nesting attempts, 93 percent produced full clutches and 76 percent yielded at least one fledgling. Successful nests on average produced 5.10 (n = 298) fledglings per first brood, 5.35 (n = 34) per second brood, and 3.56 (n = 9) per replacement brood. Number of fledglings per nest was not significantly different between first and second broods, but both first and second produced significantly more fledglings than did replacement broods. Second clutches were more likely to produce fledglings than either first or replacement clutches. Sixty-six percent of all eggs laid hatched and 58 percent produced fledglings. Of eggs that hatched, 87 percent survived to fledging. 13 March was the mean date for initiation of egg laying and latest second clutches hatched on 4 October.

I documented lifetime reproductive success (LRS) for 262 owls. Mean age of first breeding by marked individuals was 1.06 years (range <1-3), mean number of years breeding was 1.30 (range 1-7), and mean number of years breeding successfully was 1.03 (0-6). Eleven percent of these owl pairs produced two broods in one year. Mean number of eggs produced in a lifetime was 9.76 (range 1-66) and mean number of young fledged was 5.58 (range 0-50). Eight percent of the females laid 25 percent of the population's eggs and 55 percent laid 75 percent. Of females that laid eggs, 22 percent produced no fledglings. Twelve percent of females left breeding descendants in the population with up to four generations traced; the number of direct descendants from these females ranged from 3-69. The number of eggs laid in lifetimes was significantly correlated with life spans and with the number of fledglings produced. Breeding age of females did not strongly affect clutch size nor the number of fledglings produced in a breeding season. Habitat variability did not affect LRS, but nest sites used often had higher nesting success. Severity of winter weather had a strong influence on LRS through mortality of adults, reduction in clutch size and in the likelihood of producing two broods in one season. Age that breeding began and the sex of Barn Owls had very little influence on individual LRS.

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Flammulated Owls (*Otus flammeolus*) Breeding in Deciduous Forests

Carl D. Marti[1]

Abstract.—The first studies of nesting Flammulated Owls (*Otus flammeolus*) established the idea that the species needs ponderosa pine (*Pinus ponderosa*) forests for breeding. In northern Utah, Flammulated Owls nested in montane deciduous forests dominated by quaking aspen (*Populus tremuloides*). No pines were present but scattered firs (*Abies* and *Pseudotsuga* spp.) were on the study plot and groves of firs existed nearby. Using nest boxes, Flammulated Owls nested 34 times in 5 years (1992-1996). Sixty-five percent of nests produced fledglings. Mean clutch size was 2.6 (range 2-4). On average, 2.1 young fledged per successful nest, and 1.3 were produced per nest attempt overall.

The Flammulated Owl (*Otus flammeolus*) is thought to be a common species in western montane forests. Little is known about its biology, but it possesses some characteristics unusual in owls: (1) has a small clutch size for its body mass, (2) is migratory, and (3) is almost entirely insectivorous (McCallum 1994). The earliest studies of Flammulated Owl nesting were done in forests where ponderosa pine (*Pinus ponderosa*) was a major species (Bull *et al.* 1990, Goggans 1986, McCallum *et al.* 1995, Reynolds and Linkhart 1987). Reynolds and Linkhart (1992) noted that all but one of the nests reported in the literature to that time were in stands containing at least some ponderosa pine. However, more recent studies have found Flammulated Owls nesting in fir (*Abies* spp.) and mixed deciduous forests (Powers *et al.* 1996).

Ponderosa pine does not occur in northern Utah, but Flammulated Owls nest there at high densities, at least locally. In this paper I present a preliminary report on the reproductive biology of Flammulated Owls nesting in a deciduous forest, including information on breeding dates, reproductive performance, and site reuse.

METHODS

Study Area

I studied Flammulated Owls on the Cache National Forest 5.6 km east of Ogden, Weber County, Utah, at elevations ranging from 1,920-1,980 m. The site is on the eastern face of the Wasatch mountain range at the base of steeper slopes rising to 3,000 m. Both coniferous and deciduous forests are present adjacent to open areas containing shrubs, grasses, forbs, and wetlands. My studies were done in a deciduous forest dominated by quaking aspen (*Populus tremuloides*). Scattered individuals and small groves of Gambel's oak (*Quercus gambelii*), bigtooth maple (*Acer grandidentatum*), and Rocky Mountain maple (*Acer glabrum*) were also present. No pines were extant but scattered Douglas-fir (*Pseudotsuga menziesii*) and white fir (*Abies concolor*) were on the study plot, and groves of firs existed nearby on steeper slopes. Understory was dense and included bracken fern (*Pteridium aquilinum*), western coneflower (*Rudbeckia occidentalis*), slender wheatgrass (*Agropyron trachycaulum*), sticky geranium (*Geranium viscosissimum*), mountain snowberry (*Symphoricarpos oreophilus*), blue elderberry (*Sambucus cerulea*), and nettleleaf gianthyssop (*Agastache urticifolia*).

Nest boxes for Flammulated Owls were attached to living trees, mostly aspen, at heights of 3-4.5 m. Boxes were made from 20-mm-thick pine boards, and most of them had internal dimensions of 19 x 23 x 32 cm with an entrance hole of 7.5 cm. The remaining 10 boxes measured 15 x 19 x 30 cm with an entrance hole of 6.5 cm. Boxes were positioned to permit a flight path clear of vegetation to the box opening. Fifteen boxes were available in the first year (1992), and additional boxes were added each year to a total of 41 in 1996.

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Data Collection

I visited all boxes each spring soon after snow melt, usually in early May, to remove unused squirrel nests (active squirrel nests were left), and to document the first use by owls. I revisited boxes periodically through July to record numbers of eggs and young and to band the adult females and nestlings.

RESULTS

Flammulated Owls arrived on the study area from early to mid-May (USDA Forest Service unpubl. data), and most eggs were laid in the first 2 weeks of June. Eggs found on two occasions in mid-July might have been renests. Most eggs hatched in the first 2 weeks of July, and most young fledged by the end of July.

From 1992 through 1996, I documented 34 nesting attempts where at least one egg was laid (all in nest boxes) of which 79 percent resulted in complete clutches. Twenty-two nests (65 percent of nest attempts) produced fledglings. Five nest failures were due to predation upon the eggs or young, probably by northern flying squirrels (*Glaucomys sabrinus*). Causes of the remaining failures were not known—four occurred at the incubation stage and two at the nestling stage. Mean size of complete clutches was 2.6 eggs (fig. 1). Number of nestlings averaged 2.4 (fig. 2), and 2.1 young fledged per successful nest (fig. 3). Sixty-five percent of eggs laid in complete clutches survived to the age of fledging. Three-egg clutches were the most productive—54 percent of all fledglings came from three-egg clutches, while two-egg clutches produced 28 percent, and four-egg clutches only 8 percent of the fledglings. Furthermore, 45 percent of three-egg clutches produced three fledglings,

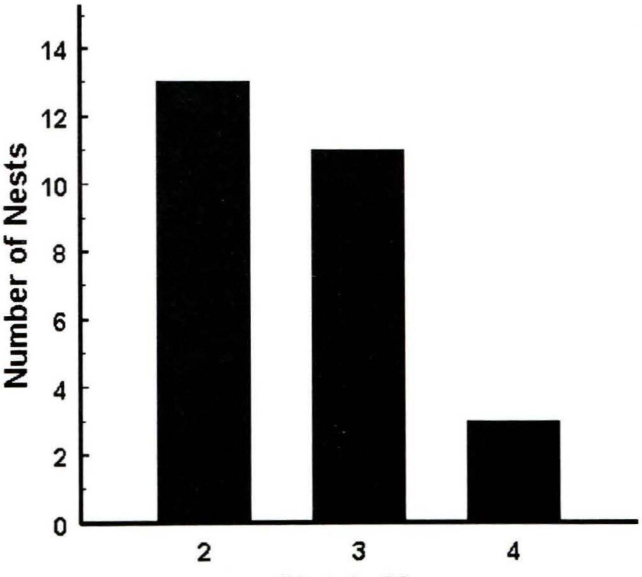

Figure 1.--*Flammulated Owl (*Otus flammeolus*) clutch size in northern Utah.*

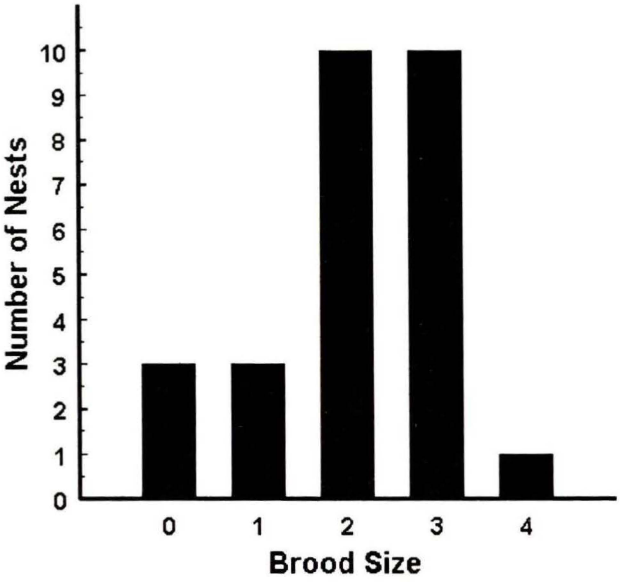

Figure 2.—*Flammulated Owl (*Otus flammeolus*) brood size in northern Utah.*

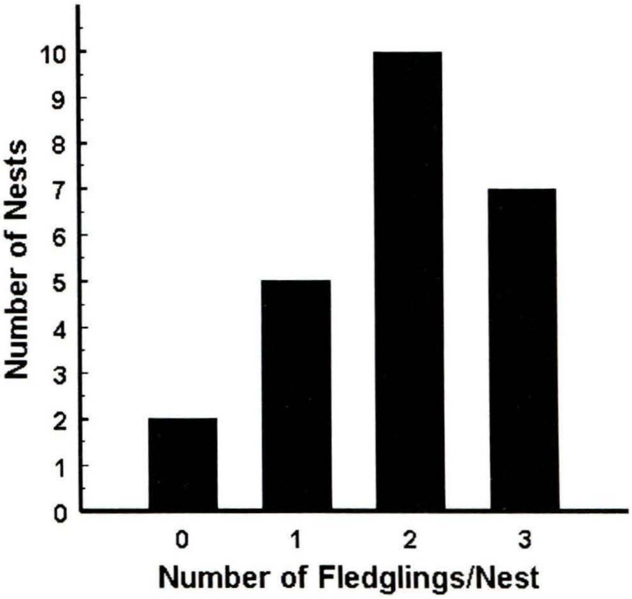

Figure 3.—*Fledglings per nest in Flammulated Owls (*Otus flammeolus*) in northern Utah.*

and only one three-egg clutch failed to produce any. Only 33 percent of two-egg clutches resulted in two fledglings, and three of them failed to produce fledglings. Although none of the four-egg clutches yielded four fledglings, one resulted in two and two produced three. Over the 5 years, 1.3 fledglings were produced per nesting attempt. Table 1 lists productivity data and nest site usage by year.

Of boxes available for 5 years, Flammulated Owls used two for 2 years and three for 3 years each. Three boxes available for 3 years were used for 2 years each. Twenty-seven percent of boxes available for 4 years were never used by Flammulated Owls, but two of those boxes were occupied by Northern Saw-whet Owls (*Aegolius acadicus*). Saw-whet Owls also nested in three boxes that Flammulated Owls used in alternate years, so the two owl species were not segregated by nest site location. Northern flying squirrels also built nests in several boxes in alternate years. Saw-whet Owls and flying squirrels both occupied nest sites before Flammulated Owls arrived on the area, thus potentially preventing Flammulated Owls from using some boxes.

I banded 46 nestlings but none were encountered again on the study area—apparently they did not join their natal population as breeders. Fourteen females were banded as breeders and four were recaptured in later years. One bred twice in consecutive years in the same nest box; the other three moved to boxes 50-150 m distant from their original nest site.

DISCUSSION

My northern Utah study area is outside the range of ponderosa pine and is quite different in vegetative composition compared with sites where Flammulated Owls have been studied in Colorado (Reynolds and Linkhart 1987), New Mexico (McCallum *et al.* 1995), and Oregon (Bull *et al.* 1990, Goggans 1986). My findings and those of Powers *et al.* (1996) show clearly that ponderosa pine is not the only vegetative type that supports breeding populations.

Clutch and brood sizes on my site were comparable to those measured in other areas (table 2), but productivity might be lower. Only 1.3 fledglings were produced per nest in Utah compared with 1.5 in New Mexico (McCallum *et al.* 1995), and 2.3 per nest in Colorado (Reynolds and Linkhart 1987). In contrast, only five four-egg clutches had been documented previously for Flammulated Owls throughout their range (McCallum 1994). That fact makes the three four-egg clutches that I found especially noteworthy.

Reynolds and Linkhart (1987) and McCallum *et al.* (1995) also observed that Flammulated Owls hatched on their study sites did not become breeders near their natal sites. Likewise, they and Goggans (1986) noted that birds banded as breeders often returned to the study area, sometimes to the same nest site in subsequent years.

Several authors noted that Flammulated Owls appear to form clusters of breeding pairs with

Table 1.—*Nest site usage and productivity by year for Flammulated Owls (*Otus flammeolus*) in northern Utah.*

Year	Boxes available	Boxes used	Nests successful	Mean clutch size[1]	Mean number of fledglings[2]
1992	15	6	2	?	1.5
1993	15	5	2	2.0	0.75
1994	37	8	7	2.4	2.0
1995	37	6	4	2.5	2.5
1996	41	9	7	2.9	2.3

[1] In complete clutches.

[2] In successful nests.

Table 2.—*Productivity of Flammulated Owls in the western United States* (tabular values are means with ranges in parentheses).

Location	N nests	Clutch	Nestlings	Fledglings
Colorado[1]	?[6]	2.7 (2-3) n = 11	2.4 (1-3) n = 26	2.6 (1-3) n = 23
Idaho[2]	24	?	2.3 (2-3) n = 9	?
New Mexico[3]	14	2.3 (2-3) n= 11	2.2 (?) n = 11	1.8 (?) n = 11
Oregon[4]	19	2.7 (2-3) n = 7	?	2.7 (2-3) n = 9
Utah[5]	34	2.6 (2-4) n = 27	2.4 (1-3) n = 24	2.1 (1-3) n = 22

[1] Reynolds and Linkhart (1987)
[2] Powers *et al.* (1996)
[3] McCallum *et al.* (1995)
[4] Goggans (1986)
[5] This study
[6] Value not available

areas of unoccupied habitat between clusters (McCallum 1994 and references therein). The same pattern appeared in northern Utah. My study area contained one such cluster, but other groves of aspens and firs in the vicinity had little, if any, use by Flammulated Owls (USDA Forest Service, unpubl. data). One aspen grove, in particular, located 2 km from my study area and closely resembling it in vegetative structure apparently was not used at all by Flammulated Owls. Another cluster of Flammulated Owls breeding in an aspen grove about 22 km southwest of my study area was reported by Smith (1991). Flammulated Owls in Utah do use vegetative communities other than pure deciduous forests for nesting. Smith (1991) found nests in a mixed coniferous forest in northern Utah, and auditory surveys have also detected males calling in coniferous forests of northern Utah (USDA Forest Service, unpubl. data). Many questions are yet unanswered about nesting habitat selection by Flammulated Owls. Availability of nesting cavities and density of prey in areas used for nesting and areas not used are two factors that need to be investigated.

This study shows that Flammulated Owls can reproduce successfully in deciduous as well as coniferous forests. Because the species is considered sensitive by the USDA Forest Service in the Northern, Rocky Mountain, Southwest-ern, and Intermountain regions (Verner 1994), surveys are being conducted in many localities to document its presence and population den-sity. Such surveys should include pure decid-uous stands in addition to coniferous and mixed forests.

ACKNOWLEDGMENTS

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LITERATURE CITED

Bull, E.L.; Wright, A.L.; Henjum, M.G. 1990. Nesting habitat of Flammulated Owls in Oregon. Journal of Raptor Research. 24: 52-55.

Goggans, R. 1986. Habitat use by Flammulated Owls in northeastern Oregon. Corvallis, OR: Oregon State University. 54 p. M.S. thesis.

McCallum, D.A. 1994. Flammulated Owl (*Otus flammeolus*). In: The birds of North America. No. 93. Philadelphia, PA: American Ornithologists' Union; Washington, DC: Academy of Natural Science. 23 p.

McCallum, D.A.; Gehlbach, F.R.; Webb, S.W. 1995. Life history and ecology of Flammulated Owls in a marginal New Mexico population. Wilson Bulletin. 107: 530-537.

Powers, L.R.; Dale, A.; Gaede, P.A.; Rodes, C.; Nelson, L.; Dean, J.J.; May, J.D. 1996. Nesting and food habits of the Flammulated Owl (*Otus flammeolus*) in southcentral Idaho. Journal of Raptor Research. 30: 15-20.

Reynolds, R.T.; Linkhart, B.D. 1987. The nesting biology of Flammulated Owls in Colorado. In: Nero, R.W.; Clark, R.J.; Knapton, R.J.; Hamre, R.H., eds. Biology and conservation of northern forest owls; Symposium proceedings; 1987 February 3-7; Winnipeg, MB. Gen. Tech. Rep. RM-142. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 239-248.

Reynolds, R.T.; Linkhart, B.D. 1992. Flammulated Owls in ponderosa pine: evidence of preference for old growth. In: Old-growth forests in the southwest and Rocky Mountain regions. Gen. Tech. Rep. RM-213. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station.

Smith, V.A. 1991. Some notes on Flammulated Owl nesting behavior in northern Utah. Utah Birds. 7: 65-70.

Verner, J. 1994. Current management situation: Flammulated Owls. In: Hayward, G.D.; Verner, J., tech. eds. Flammulated, Boreal, and Great Gray Owls in the United States: a technical conservation assess-ment. Gen. Tech. Rep. RM-253. Fort Collins, CO: U.S. Department of Agricul-ture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 213 p.

Barred Owl (*Strix varia*) Nest Site Characteristics in the Boreal Forest of Saskatchewan, Canada

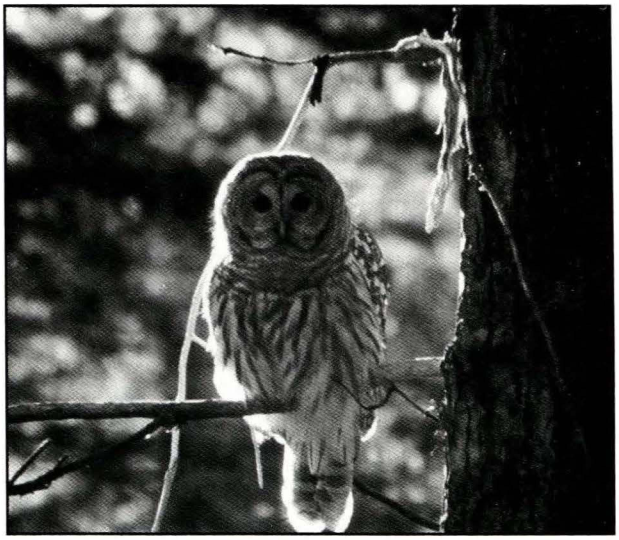
Kurt M. Mazur, Paul C. James, and Shanna D. Frith[1]

Abstract.—Between 1994 and 1996 we located 15 active Barred Owl (*Strix varia*) nests in the boreal forest of central Saskatchewan, Canada. Eighty-seven percent of Barred Owl nests were located within old mixedwood forest stands. Nest tree species included white spruce (*Picea glauca*), trembling aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), and white birch (*Betula papyrifera*). The majority of nests were within natural cavities (67 percent), and the majority of nest trees were live (67 percent). Nest trees were of large diameter, averaging 47.4 cm. Nest site availability appears to be an important factor for this species reliance on old forest.

Raptor populations are in part limited by the availability of suitable nest sites (Newton 1979). Owls are further affected by nest site availability as they do not construct a nest as a rule (Johnsgard 1988). This is especially true for those species which rely on existing cavities to nest in. Barred Owls (*Strix varia*) primarily nest in tree cavities, but will also use stick nests, and have been noted to nest on the ground (Bent 1938, Johnsgard 1988, Robertson 1959). In the boreal forest of Canada few Barred Owl nest records exist. Our objective was to describe Barred Owl nests within the boreal forest of Saskatchewan.

STUDY AREA AND METHODS

The research was conducted from March 1994 to August 1996 within the southern boreal forest of Saskatchewan, Canada (53°35'-54°15'N, 105°05'-106°45'W). The approximately 400,000 ha study area encompassed the Prince Albert Model Forest including a portion of Prince Albert National Park. The common tree species in the study area included trembling aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), white birch (*Betula papyrifera*), white spruce (*Picea glauca*), black spruce (*Picea mariana*), tamarack (*Larix laricina*), jack pine (*Pinus banksiana*), and balsam fir (*Abies balsamea*). The habitat included pure deciduous, mixed coniferous/deciduous, and pure coniferous forest, muskeg, and shrub lands. Elevation ranged from 490 to 698 m. The topography is gently rolling, interspersed with numerous lakes and creeks. The climate is boreal continental, with an average annual precipitation of 401 mm; 281 mm as rain and 120 mm as snow; July and January temperatures average 17.6°C and -19.7°C, respectively, with annual extreme temperatures of 36.1°C and -48.3°C (Environment Canada Parks 1986).



Kurt Mazur

*Barred Owl (*Strix varia*).*

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Nests were located either by following a radio-marked female Barred Owl to a nest, or by searching the area where a pair of Barred Owls had been detected during call-playback surveys (Frith *et al.* 1997). The forest stand that each nest fell within was classified according to a scheme created using the updated (1993) version of the existing forest inventories for Prince Albert National Park (Padbury *et al.* 1978) and the Saskatchewan Northern Provincial Forest (Lindenas 1985) (table 1). Nest tree species and its status (dead or live) was recorded, as well as the type of nest structure. Nest structures were classified as either cavity or platform, where cavity included a tree cavity formed by the top of a tree or limb breaking off, and a platform included stick nests. Nest tree height and nest structure height were measured with a clinometer (Suunto, Espoo, Finland). Nest tree diameter at breast height (d.b.h.) and distance to the nearest all-weather road were measured.

RESULTS

Fifteen active Barred Owl nests were located between 1994 and 1996 (table 2a). Nest sites were located almost exclusively in old mixedwood forest, with one nest in old coniferous forest and one in mature deciduous forest (table 2a). Nest tree species was variable, with five nests in white spruce, five in trembling aspen, four in balsam poplar, and one in a white birch. The majority of the nest trees were live (10 of 15; 67 percent). Sixty-seven percent (10) of nests were tree cavities, with the remainder on platforms (table 2a). Six of the cavity nests were formed where the top of the tree broke off leaving a cavity in the snag. The other four were formed where a limb broke off, likely from rot. In all cavity nests the owl was entirely concealed from view from the ground. Two of the platform nests were old stick nests (Accipitridae and Corvidae). These stick nests were used by the same owl in consecutive years. Red squirrel (*Tamiasciurus hudsonicus*) nests constituted two platform nests, where the owl sat on top of the structure, and one owl nested on top of a witch's broom (dense branching caused by *Arceuthobium* spp.) in a white spruce tree. Nest tree height averaged 18.8 m and nest height averaged 13.3 m (table 2b). Nest trees were large, averaging 47.4 cm d.b.h. The proximity to an all-weather road was quite variable ranging from 25 m to 2,000 m (average 430 m; table 2b).

Reuse of nests over years varied among owls. Summit and Beaver Glen Owls used the same nest for 2 consecutive years, while Prospect and Spruce River Owls used different nests within the same territory in consecutive years. The Whelan Bay female shifted her territory after 1994, and subsequently used a different nest in 1995, and also used a different nest in 1996 while remaining on the same territory. All other owls were only monitored for 1 year. Of the 15 nests found, three (20 percent) had fallen down within the 3-year study period.

Table 1.—*Habitat classification by habitat cover type and age in the boreal forest of Saskatchewan, Canada.*

Habitat type	Cover vegetation description
Deciduous[1]	Trembling aspen +/or balsam poplar +/or white birch (<20 percent conifer)
Mixedwood[1]	Combination of deciduous and coniferous species: trembling aspen, balsam poplar, white birch, white spruce, black spruce, jack pine, balsam fir (≥ 20 percent conifer, ≥ 20 percent deciduous)
Coniferous[1]	White spruce +/or black spruce+/or jack pine +/or tamarack +/or balsam fir (<20 percent deciduous)
Treed muskeg	Black spruce +/or tamarack, excessive moisture and retarded tree growth

[1] Could occur in three age classes: Young (<50 years). Mature (50-79 years), and Old (80+ years).

Table 2a.—*Characteristics of 15 Barred Owl (*Strix varia*) nests in the boreal forest of Saskatchewan, Canada.*

Owl	**Nest stand**	**Nest tree species**	**Nest tree status**	**Nest type**
Prospect 95	Old mixedwood	White spruce	Live	Platform (witch's broom)
Prospect 96	Old mixedwood	White spruce	Live	Platform (squirrel nest)
Summit	Old mixedwood	White spruce	Dead	Cavity (broken top)
Spruce River 94	Old mixedwood	White spruce	Live	Cavity (broken top)
Candle Lake	Old mixedwood	White spruce	Live	Platform (squirrel nest)
Spruce River 95	Mature deciduous	White birch	Live	Cavity (broken top)
Beaver Glen	Old mixedwood	Balsam poplar	Dead	Cavity (broken top)
Heart Lakes 94	Old mixedwood	Balsam poplar	Live	Cavity (broken limb)
Heart Lakes 96	Old mixedwood	Balsam poplar	Live	Cavity (broken limb)
Point View	Old mixedwood	Balsam poplar	Live	Cavity (broken limb)
Whelan Bay 94	Old mixedwood	Trembling aspen	Dead	Cavity (broken top)
Whelan Bay 95	Old mixedwood	Trembling aspen	Live	Platform (stick nest)
Whelan Bay 96	Old coniferous	Trembling aspen	Live	Platform (stick nest)
Whiteswan	Old mixedwood	Trembling aspen	Dead	Cavity (broken limb)
Birch Bay	Old mixedwood	Trembling aspen	Dead	Cavity (broken top)

Table 2b.—*Further characteristics of 15 Barred Owl (*Strix varia*) nests in the boreal forest of Saskatchewan, Canada.*

Owl	**Nest tree height (m)**	**Nest height (m)**	**Nest tree d.b.h. (cm)**	**Distance to road (m)**
Prospect 95	29.5	22.3	42.5	25
Prospect 96	27.4	15.9	35.6	200
Summit	14.7	12.2	74.5	1,000
Spruce River 94	16.7	14.3	59.0	50
Candle Lake	21.5	15.5	34.7	150
Spruce River 95	13.8	6.9	51.5	50
Beaver Glen	7.8	7.0	41.6	900
Heart Lakes 94	24.5	11.0	69.2	150
Heart Lakes 96	19.8	15.5	58.5	500
Point View	21.8	10.8	54.0	100
Whelan Bay 94	9.3	9.0	37.8	800
Whelan Bay 95	23.5	18.0	31.9	300
Whelan Bay 96	22.3	17.3	36.4	75
Whiteswan	19.3	14.0	48.1	2,000
Birch Bay	11.3	11.3	35.0	150
Mean (SD)	18.8 (6.2)	13.3 (4.1)	47.4 (12.8)	430.0 (525.7)

DISCUSSION

Barred Owl nests were predominantly found in old mixedwood forests. This is consistent with what has previously been recorded for this species (Bent 1938, Devereux and Mosher 1982, Johnsgard 1988). Nest sites along with prey availability are thought to be two primary features involved in raptor habitat selection (Newton 1979). The large body size (female $\bar{x}$ = 801 g) (Johnsgard 1988) of the Barred Owl demands a large tree cavity for nesting, hence a large tree. In the boreal forest of Alberta, old mixedwood forest was the only forest type found to contain both trees and snags of this size (Lee *et al.* 1995). This is likely true for our study area as well. Nest site requirements are considered the predominant factor involved in the Barred Owls' association with old forest (Devereux and Mosher 1982, Elderkin 1987, Johnsgard 1988). Elderkin (1987) found Barred Owls readily inhabiting young forest that contained nest boxes, and only located natural nests in mature forests. Mazur (1997) found Barred Owls in the boreal forest selecting old mixedwood forest for both roosting and hunting as well. The relationship between nest site availability and old forest has been established for other cavity nesting North American owls such as the Boreal Owl (*Aegolius funereus*) and the Spotted Owl (*Strix occidentalis*) (Forsman *et al.* 1984, Lane and Andersen 1995).

Although found nesting in stick nests, Barred Owls are considered to be mainly secondary tree cavity nesters (Bent 1938, Devereux and Mosher 1982, Johnsgard 1988). Two-thirds of the nests found in this study were in tree cavities, with one-third on platform type nests, suggesting some flexibility in their nesting requirements. The use of a platform nest may be a behavior imprinted on owls raised in stick nests, as suggested by Devereux and Mosher (1984). Suitable tree cavities may also be in short supply, limiting some owls to platform nests. Of the Barred Owls that used platform nests, one used a cavity (snag) 1 year and then used a stick nest the following 2 years, while another owl used a witch's broom 1 year and a squirrel nest the following year. In contrast, other owls used tree cavities exclusively.

Two Barred Owls reused nest sites over 2 years while three owls switched nests in consecutive years. Nest switching may have been a result of nest failure or predation the previous year. However, reproductive success of the nests was not monitored in this study. Devereux and Mosher (1984), reported of four nests found in 1 year, none was reused the following year. Conversely, Elderkin (1987) reported high nest site tenacity. It often appears that more than one nest is available within a Barred Owl's territory. This would provide an alternate choice for nesting if the previous nest site had fallen down or had proved susceptible to predation. Sonerud (1989) found that Tengmalm's Owl suffered lower predation by pine martens (*Martes martes*) by switching nest sites. Nest switching may be adaptive for Barred Owls in the boreal forest which are susceptible to nest predation by American pine marten (*Martes americana)* and fisher (*M. pennanti*). Barred Owl nest sites are ephemeral by their nature. Many of the trees supporting cavity nests have some degree of rot, and stick nests eventually come apart. By having more than one nest site within a territory, Barred Owls ensure that nesting attempts can be made despite the disappearance of one nest site.

The distance Barred Owl nest sites were from roads was quite variable, with many nests quite close (25 m) to roads. As surveys for Barred Owls were conducted along roads, the distance nests were from roads may not be a true representation of the Barred Owl population in the study area. Within the boreal forest, the Barred Owl's relatively narrow use of habitat for nesting makes it susceptible to alteration or loss of this habitat.

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LITERATURE CITED

Bent, A.C. 1938. Life histories of North American birds of prey, Part II. New York, NY: Dover Publishing Inc. 482 p.

Devereux, J.G.; Mosher, J.A. 1982. Nesting habits of the Barred Owl in western Maryland. Maryland Birdlife. 38: 124-126.

Devereux, J.G.; Mosher, J.A. 1984. Breeding ecology of Barred Owls in the central Appalachians. Journal of Raptor Research. 18: 49-58.

Elderkin, M.F. 1987. The breeding and feeding ecology of a Barred Owl *Strix varia* Barton population in Kings County, Nova Scotia. Wolfville, NS: Acadia University. 203 p. M.S. thesis.

Environment Canada Parks. 1986. Prince Albert National Park resource description and analysis. Winnipeg, MB: Environment Canada Parks, Prairie and Northern Region, 2 vols.

Forsman, E.D.; Meslow, E.C.; Wight, H.M. 1984. Distribution and biology of the Spotted Owl in Oregon. Wildlife Monograph. 87: 1-64.

Frith, S.D.; Mazur, K.M.; James, P.C. 1997. A method for locating Barred Owl (*Strix varia*) nests in the southern boreal forest of Saskatchewan. In: Duncan, J.; Johnson, D.; Nicholls, T., eds. Biology and conservation of owls of the northern hemisphere: 2d international symposium; 1997 February 5-9; Winnipeg, Manitoba. Gen. Tech. Rep. NC-190. St. Paul MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station: 545-547.

Johnsgard, P.A. 1988. North American owls, biology and natural history. Washington, DC: Smithsonian Institution Press. 295 p.

Lane, W.H.; Andersen, D.E. 1995. Habitat requirements for Boreal Owls in northeastern Minnesota. Final Report prepared by Minnesota Cooperative Fish and Wildlife Research Unit, University of Minnesota for North Central Forest Experiment Station St. Paul, Minnesota. 52 p.

Lee, P.C.; Crites, S.; Nietfeld, M.; Van Nguyen, H.; Stelfox, J.B. 1995. Changes in snag and down woody material characteristics in a chronosequence of aspen mixedwood forests in Alberta. In: Stelfox, J.B., ed. Relationships between stand age, stand structure, and biodiversity in aspen mixedwood forests in Alberta. Jointly published by Vegreville, AB: Alberta Environmental Center (AECV95-R1); Edmonton, AB: Canadian Forest Service (Project No. 0001A): 49-61.

Lindenas, D.G. 1985. Forest inventory interpretation and mapping manual. Forestry Branch Saskatchewan Parks and Renewable Resources.

Mazur, K.M. 1997. Spatial habitat selection by Barred Owls in the boreal forest of Saskatchewan, Canada. Regina, SK: University of Regina. 80 p. M.S. thesis.

Newton, I. 1979. Population ecology of raptors. Vermilion, SD: Buteo Books. 399 p.

Padbury, G.A.; Head, W.K.; Souster, W.E. 1978. Biophysical resource inventory of the Prince Albert National Park, Saskatchewan. Saskatoon, SK: Saskatchewan Institute of Pedology Publication S185.

Robertson, W.B. 1959. Barred Owl nesting on the ground. Auk. 76: 227-230.

Sonerud, G.A. 1989. Reduced predation by pine martens on nests of Tengmalm's Owl in relocated boxes. Animal Behaviour. 37: 332-343.

Population Densities of Northern Saw-whet Owls (*Aegolius acadicus*) in Degraded Boreal Forests of the Southern Appalachians

Timothy C. Milling[1], Matthew P. Rowe[1,2], Bennie L. Cockerel[1], Timothy A. Dellinger[1],
Johnny B. Gailes[1], and Christopher E. Hill[3]

Abstract.—A disjunct population of the Northern Saw-whet Owl (*Aegolius acadicus*) breeds in the montane spruce-fir forests of the southern Appalachian Mountains. These forests are listed as the second most endangered ecosystem in the United States, having suffered from logging and massive fir die-off from the exotic balsam woolly adelgid. We used audio playbacks to compare densities of saw-whets prior to fir die-off (1968-1969) with those now (1993-1994); numbers were almost identical, suggesting little if any impact from the adelgid. Extrapolation from our density estimates, however, show fewer than 500 pair of saw-whets in the southeastern population. Global warming, air pollution, outbreaks of new pests, and burgeoning recreational demands may further degrade these forests, leading to the possible extirpation of saw-whets from the southern Appalachians.

The Northern Saw-whet Owl (*Aegolius acadicus acadicus* Gmelin) is a widespread and common owl in the forests of southern Canada and the northern United States (Cannings 1993, Johnsgard 1988). An apparent generalist, it has been found breeding in habitats as diverse as conifer plantations, deciduous forests, and cedar bogs (Cannings 1993, Johnsgard, 1988). Two potentially isolated populations occur in the eastern United States: a mid-Atlantic disjunct on the Allegheny Plateau of eastern West Virginia and western Maryland; and a southeastern disjunct in the southern Appalachian Mountains of western North Carolina, eastern Tennessee, and southwestern Virginia (fig. 1). Both of the eastern disjuncts may represent glacial relicts (Tamashiro 1996), remnants of a more extensive boreal flora and fauna associated with the Wisconsin glacial

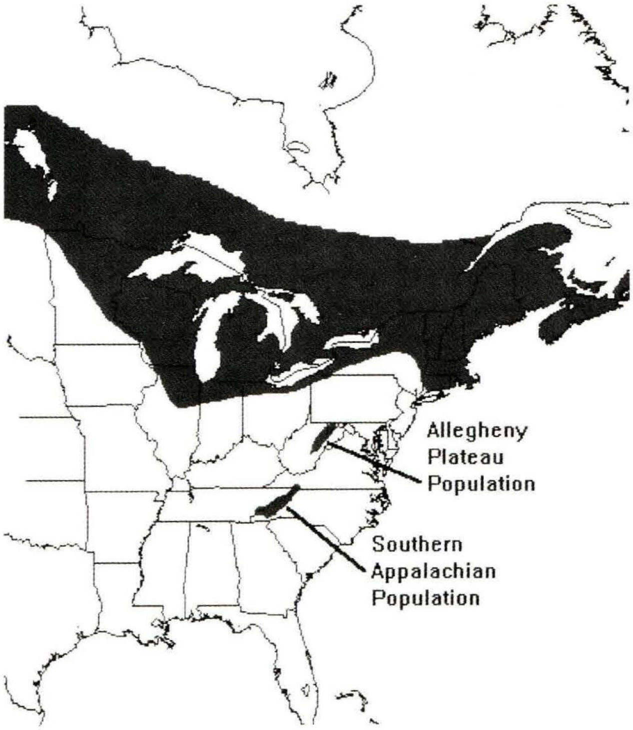

Figure 1.—*Breeding distribution of the Northern Saw-whet Owl (*Aegolius acadicus*) in the eastern United States and Canada (adapted from figure 50 in Johnsgard 1988 and figure 1 in Cannings 1993; isolation of the Allegheny Plateau population from the population in Pennsylvania/New York may be less discrete than illustrated (Gross 1992; Brinker, pers. comm.).*

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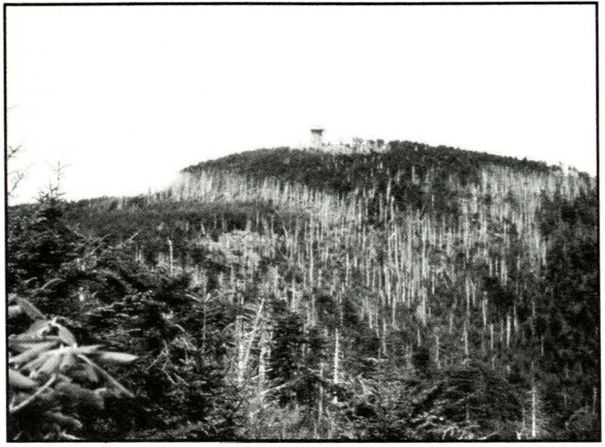
maximum of 18,000 years ago (Delcourt and Delcourt 1984, Parmalee and Klippel 1982, Wright 1981).

Unlike their northern cousins, southern Appalachian saw-whets appear to be habitat specialists, with breeding (assessed primarily by reports of territorial calling) restricted to high-elevation stands of red spruce (*Picea rubens* Sargent), Fraser fir (*Abies fraseri* (Pursh) Poiret), and associated northern hardwoods (Crutchfield 1990, Simpson 1992, Stupka 1963). The red spruce and Fraser fir are themselves glacial relicts, restricted now to elevations above 1,350 m (4,430 ft) in the southern Appalachians (Dull *et al.* 1988, White *et al.* 1993). As might be expected, the geographic isolation of southern Appalachian spruce-fir forests has produced a suite of endemic plants and animals, including at least eight endemic species and subspecies of birds (Groth 1988, Rabenold 1984). Although southern Appalachian saw-whets are not one of these eight officially-recognized avian endemics, individuals from this region are morphologically distinguishable from other populations (Tamashiro 1996), including saw-whets from the Allegheny Plateau, from the "main-range" of the northern U.S. and southern Canada, and from a distinct subspecies restricted to the Queen Charlotte Islands (*Aegolius acadicus brooksi* Fleming).

The apparent restriction of southern Appalachian saw-whets to high-elevation spruce-fir forests is worrisome, as this forest type is listed as the second-most endangered ecosystem in the U.S. (Noss and Peters 1995, White *et al.* 1993). With the retreat of the Laurentide ice sheet, spruce-fir forests became rare in the southeast, restricted to only the highest peaks in the southern Appalachians. Logging early this century decimated what little remained, with clear-cutting and slash-induced fires destroying as much as 90 percent of the virgin spruce and fir (Korstian 1937). Following logging, the forests experienced several decades of recovery, only to be threatened by the balsam woolly adelgid (*Adelges piceae* Ratzeburg), an exotic pest of fir trees brought into the United States on nursery stock from Europe. Although the adelgid was first detected on Mount Mitchell in the southern Appalachians in 1957, many of the peaks remained uninfected until the late 1960's and significant mortality of Fraser fir did not occur until the late 1970's (Dull *et al.* 1988). For example, in 1976 only 10 ha (25 acres) of fir showed heavy mortality in Great Smoky Mountains National Park, a value that had risen to 1,862 ha (4,600 acres) by 1985; 91 percent of the mature Fraser fir now stand dead in the Park (Dull *et al.* 1988). Glacial retreat, clearcutting, and the adelgid have reduced southern Appalachian spruce-fir forests to a patchy archipelago of high-elevation islands stretching from Mount Rogers in southwestern Virginia to the Great Balsam Mountains of southwestern North Carolina (fig. 2).


Tim Silver

Die-off of fir trees on Mt. Mitchell, southern Appalachian Mountains.

Have logging and exotic pests affected the southeastern population of saw-whet owls? Unfortunately, the presence of a breeding population of saw-whets in the southern Appalachians was not recognized until the 1940's (Stupka 1963), decades after the spruce-fir had been logged. Impacts from the adelgid, however, might be assessed. Auditory playbacks have proven useful for determining the abundance of rare or elusive bird species (Fuller and Mosher 1981, Johnson *et al.* 1981), and have been used successfully for censusing saw-whet owls (Palmer 1987, Swengel and Swengel 1987). An early but unrecognized pioneer of this technique is Marcus Simpson, Jr. Simpson (1972) used whistled imitations of the saw-whet advertisement/territorial call (Cannings 1993) to census saw-whets in the Great Balsam Mountains of the southern Appalachians during the breeding seasons of 1968-1971, prior to adelgid-induced fir mortality in this range. The balsam woolly adelgid did not arrive in the Balsam Mountains until 1968, and death of the fir did not begin until the mid to late 1970's (Dull *et al.* 1988), as it takes 5-10

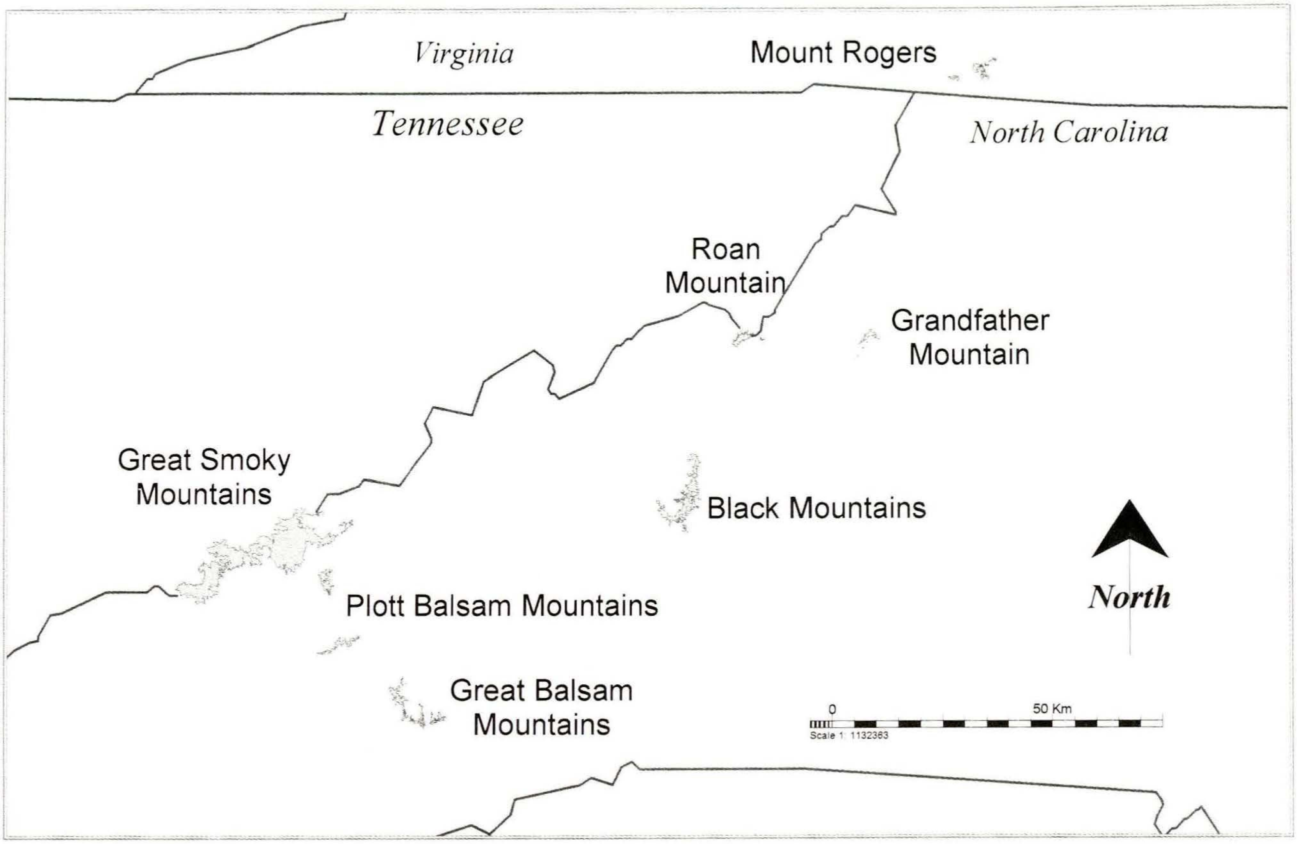


Figure 2.—*Distribution of spruce-fir forests in the southern Appalachian mountains (adapted from figure 5 in Dull* et al. *1988). Our study sites were located on Roan Mountain, the Black Mountains, and the Great Balsam Mountains.*

years before an adult fir is killed by the adelgid (Busing *et al.* 1988). A post-adelgid census of saw-whets in the Great Balsam Mountains could elucidate the impact of fir die-off on saw-whet densities in this disjunct, southeastern population.

This paper is part of a larger, ongoing investigation begun in 1991 exploring the conservation biology of southern Appalachian saw-whets. The research reported here has two main goals: first, to compare densities of saw-whet owls in the Great Balsam range of the southern Appalachians prior to and following adelgid-induced fir die-off; and second, to estimate the number of saw-whets in the disjunct southern Appalachian population.

METHODS

Study Areas

Census work was conducted from February to August in 1993 and 1994 on three mountain ranges in the southern Appalachians (fig. 2), each of which was known from published reports and our own research to harbor breeding saw-whets: Roan Mountain; the Black Mountains, including Mt. Mitchell; and the Great Balsam Mountains. A core group of high elevation forests, predominantly boreal spruce-fir forests and their lower-elevation ecotone with northern hardwoods, were identified for census during both years. We took advantage of the Blue Ridge Parkway for censusing the Black and Balsam Mountains, as this national roadway runs along the mountain ridges in both areas and provides excellent access to both the high-elevation spruce-fir forests and, in valleys and saddles between peaks, to lower-elevation hardwood and cove forests (see Simpson 1972). Surveys on Roan Mountain were conducted by driving and hiking along U.S. Forest Service access roads and hiking trails.

Census Method

We used the strip-map census technique (Emlen 1984), with a quantitative modification outlined below, to estimate the number of territorial saw-whets at each study site each year. Taped playbacks of saw-whet advertisement calls were broadcast along roads and trails to elicit vocal responses from owls. These playbacks were broadcast at intervals of 0.5 to 0.8 km (0.3 to 0.5 mi), depending on geography (e.g., closer intervals were required when playback locations were separated by a ridge line, while longer intervals could be used when surveying around a cove). At each broadcast location, census takers would listen for calling owls for 2 minutes, broadcast the playback intermittently for 5 minutes, then listen another 2 minutes for any response. Owls responding to playbacks or heard calling spontaneously (unprompted) were noted and the location mapped onto 7.5 minute USGS topographic maps. Saw-whets characteristically responded to the "tooting" advertisement call in kind, although whines (Cannings 1993, Hill 1995) were occasionally reported. We assume that most replies were from male saw-whets on, or in the process of establishing, their territories (Cannings 1993, Hill 1995, Otter 1996, Palmer 1987).

Changes of a given owl's calling site from night to night could be incorrectly designated as those of two owls and thus inflate the number of male saw-whets estimated to be holding territories near a particular playback station. Census takers therefore attempted to map the specific tree stand from which an owl responded (hereafter referred to as a "calling site"). This information was used to identify clusters of vocal activity (hereafter referred to as "calling clusters") over the course of the breeding season. Thus, our calling clusters are similar to Emlen's (1984) "point clusters" and Swengel and Swengel's (1987) "composite calling stations." We did, however, try to define our calling clusters in a more quantitative manner than has been typical of most spot-mapping and strip-mapping census techniques. Unless it could be determined that different individuals vocalized from a given calling cluster (e.g., antiphonal calling by two owls from the same cluster), calling sites mapped on different evenings less than 0.5 km (0.3 mi) from the center of a calling cluster were considered responses from the same owl. Cannings (1993) estimates that breeding densities of saw-whets in optimal habitat may reach one pair/km^2. Thus, a cluster of calling sites that fall within a half km radius are likely to be from the same male. The use of vocal "signatures" could, in future studies, further reduce the ambiguity of assigning a calling cluster to a specific owl (Hill 1995, Otter 1996).

In order to reduce the likelihood of incorrectly designating calls from transient owls as those of residents holding territory, only owls heard calling from the same calling cluster on 2 or more census nights of more than 7 days apart were assumed to be residents holding territory. Thus, our operational definition of a "territory" is the presence, during the breeding season, of a calling saw-whet in a circumscribed area (0.5 km radius) for more than 1 week. With the exception of our more quantitative method for identifying calling clusters, this definition is comparable to that employed by Simpson (1972) for his earlier census work in the Great Balsam Mountains.

Forest Classification, Mapping, and Density Analyses

We classified forests bordering the census transects into four categories: (1) high elevation boreal forests dominated by red spruce and Fraser fir; (2) high elevation boreal-ecotone forest of spruce-fir mixed with northern hardwoods, primarily yellow birch (*Betula alleghaniensis* Britt.), red maple (*Acer rubrum* L.), and American beech (*Fagus grandifolia* Ehrhart); (3) mid-elevation northern hardwood forests dominated by birch, maple, beech, and occasionally northern red oak (*Quercus rubra* L.); and (4) cove forest, typically composed of yellow buckeye (*Aesculus flava* Solander), Fraser magnolia (*Magnolia fraseri* Walt.), cucumber tree (*Magnolia acuminata* L.), basswood (*Tilia americana* L.), and red maple mixed with Eastern hemlock (*Tsuga canadensis* L.). The distributions of these four forest types along census routes were identified using 1988-1989 USGS high-altitude infrared aerial photographs, and were then plotted on USGS 7.5 minute topo maps. Forest-types along census routes were ground checked to correct inconsistencies in aerial photo interpretation.

Because proportions of each forest type were not equal at each site, and each forest type was not censused an equal number of nights or for an equal number of hours, we calculated relative occurrence by dividing the number of owls heard in each forest type by the total time that forest type was censused. The density of saw-whets in each forest type was estimated for each study site each year, with the exception of the Roan Mountain study area which was not sufficiently surveyed in 1994. Densities were calculated by dividing the total length of the censused forest type by the number of territories in that forest type that year.

Detailed maps of the boreal forest present on each mountain range in the southern Appalachians are presented in Dull *et al.* (1988). These maps were digitized for each of our three study areas. The roads and trails we used for our playbacks were overlaid on these maps. The distribution of spruce-fir forests in the southern Appalachians is not only fragmented across ranges, but also is quite narrow in any given range; i.e., in the southern Appalachians, spruce and fir are limited to elevations above 1,350 m (4,430 ft), and thus their distribution usually follows the contours of high-elevation ridge lines. Indeed, the major forest types exhibit a noticeable "zonation" in the southern Appalachians (Simpson 1992, White *et al.* 1993): fir grows in relatively pure stands only on the highest peaks (> 1,800 m, or 5,900 ft); mixed fir and spruce occur below 1,800 m, with fir giving way to spruce at lower elevations; the transition between spruce-fir and northern hardwoods occurs at elevations between 1,400 -1,680 m (4,593-5,249 ft); northern hardwoods themselves give way to southern oak-hickory forests below 1,300 m (4,265 ft); cove forests occur in the moist drainages along the mid to lower slopes at elevations up to 1,372 m (4,500 ft). Thus, in areas where our census route (e.g., the Blue Ridge Parkway) traversed a mountain below the ridge line, playbacks carried all the way from the fir-dominated ridge above us down into the oak-hickory carpeted valleys below (pers. observ.). When a survey route followed a ridge line, playbacks were audible down both slopes. We could neither hear a playback, nor did playbacks generate an audible response from owls, from over a ridge line.

Owl densities were therefore calculated by first identifying the area effectively censused on each side of our roughly linear transects. This area was delimited using the detection-threshold distance technique (Emlen 1984), which we determined to be a strip approximately 1.2 km (0.75 mi) in width. Where a strip of this width extended beyond terrain barriers that would interfere with hearing an owl's response (e.g., over ridge lines), the area beyond those barriers was eliminated from our estimates of total area censused. Relative densities of saw-whets in each of the three surveyed mountain ranges were computed by dividing the number of identified territories by the area censused. Because saw-whets are restricted almost exclusively to boreal and ecotone forests (Simpson 1972, 1992; and see Results below), and the extent of this forest type is known (Saunders 1979, cited in White *et al.* 1993; Dull *et al.* 1988) the absolute size of the saw-whet population in the southern Appalachians was estimated by extrapolating from relative densities.

RESULTS

Seasonality

A total of 227 census hours generated 159 saw-whet responses. Of the 227 census hours, 143.25 were from 1993 and 83.75 from 1994.

The peak calling period for saw-whets in the southern Appalachians has been reported to be between late March and mid-June (Alsop 1991, Simpson 1992). Our data support this observation. Although we have heard spontaneous, unprompted calling during calm nights at all times of the year, the earliest responses during our playback work occurred on 11 March 1993 and 18 February 1994. Both of these records are from the Great Balsam Mountains, the southernmost of our three study sites and, indeed, the southern limit of spruce-fir forest in the Appalachians. The number of owls heard calling per census increased to a maximum between mid-April and late May. The latest seasonal record of spontaneous calling was 25 June 1994, although owls continued to respond to playbacks throughout the census period. There appears to be a second bout of calling, and concomitantly an increased responsiveness to playbacks, in September and October (unpubl. data; see also Cannings 1993), perhaps due to dispersal of the young in the fall.

Spontaneous calling of saw-whets made playbacks virtually unnecessary during the peak period from mid-April to late May. Males would commonly call for hours from locations within their territories. Peak nights of vocal activity were on 16 and 27 May 1993, and 20 and 24 April 1994. During these periods, owls in adjacent territories would almost invariably be calling, such that a string of owls could be heard for 4.8 to 6.4 km (3 to 4 miles) along the transect route. On 27 May 1993, for example, 7 owls were heard simultaneously calling along a 6 km (3.7 mi) section of the Blue Ridge Parkway in the Great Balsam Mountains.

The earliest dates and the period of peak calling differed between years, with 1993 lagging behind 1994 by approximately 1 month. March 1993 was severe, with the so-called "storm of the century" bringing record snows and record low temperatures during the middle of the month (e.g., -23°C on 15 March 1993; National Weather Service data from Banner Elk, NC). Deep snow and cold temperatures may have delayed nesting and interrupted territorial establishment.

Density Per Forest Type

A total length of 86.7 km (53.9 mi) of forest transects was repeatedly censused in 1993 and 96.2 km (59.8 mi) in 1994. The boreal and boreal-ecotone forests comprised 70 percent of the length censused in 1993 and 61 percent in 1994. Northern hardwood forests comprised 22 and 39 percent of the census length for the 2 years respectively. Cove forest comprised only 8 percent of the length censused in 1993 and was not censused in 1994.

Saw-whet owls called almost exclusively from high elevation boreal and boreal-ecotone forests. Indeed, over 90 percent of the 159 responses were from sites higher than 1,524 m (5,000 ft) in elevation (table 1). Broken down by mountain range and year, the proportions of calling sites located in boreal or boreal-ecotone forests were: Black Mountains, 1993 - 95 percent, 1994 - 100 percent; Great Balsam Mountains, 1993 - 100 percent, 1994 - 84 percent; Roan Mountain, 100 percent both years. The remainder of calling sites were located in northern hardwood forests; owls were never heard responding from cove forests. The relative occurrence of saw-whets per forest type (i.e., responses per habitat type per census hour) are shown in table 2. Two points are obvious from this table. First, owls called from more sites than there were territories, an expected result if calls are given from transient owls or if territorial establishment requires some adjustment. And second, both the number of calling sites and the eventual number of established territories were greater than expected in spruce-fir and spruce-fir/ecotone forests, and lower than expected in northern hardwoods or forests. These differences are highly significant for calling sites ($\chi^2 = 24.03$, df = 3, $p < 0.0005$; Feldman *et al.* 1987), and

Table 1.—*Distribution by elevation for 159 Northern Saw-whet Owl (*Aegolius acadicus*) responses recorded during our surveys (1993-1994) in North Carolina. Elevations listed by 500 ft (152 m) increments; thus, we heard only a single saw-whet response in the Black Mountains at an elevation between 4,000-4,499 ft, five responses between 4,500-4,999 ft, etc. Cells lacking entries indicate elevations that were not censused.*

Mountain range	**Elevation (ft)**						
	3,500	**4,000**	**4,500**	**5,000**	**5,500**	**6,000**	**6,500**
Blacks[1]	0	1	5	18	12	22	5
Balsams	0	0	6	21	39	6	NA[3]
Roan[2]					24	0	NA[3]

[1] Surveys in the Black Mountains actually extended down to 3,177 ft (968 m), but no responses were heard below 4,460 ft (1,359 m).

[2] Systematic, altitudinal surveys of Roan Mountain were not part of the census design during 1993 or 1994; however, a low-elevation (2,840 ft; 866 m) hemlock forest was repeatedly surveyed and no saw-whets were discovered. Moreover, altitudinal surveys conducted during 1995 and 1996 found no saw-whets below 5,200 ft (1,585 m).

[3] Maximum elevation in the Great Balsam Mountains is 6,410 ft (1,954 m) and on Roan Mountain it is 6,285 ft (1,916 m).

Table 2.—*Relative occurrence of Northern Saw-whet Owls (*Aegolius acadicus*) by forest type (i.e., the number of calling sites and the number of territories per habitat type per hour of census) (1993-1994), North Carolina.*

Forest type	Calling sites per hour	Territories per hour
Spruce-fir	1.4	0.36
Spruce-fir/northern hardwood ecotone	1.1	0.27
Northern hardwood	0.3	0.03
Cove forest	0.0	0.00

approach significance for territories ($\chi^2 = 6.31$, df = 3, $p < 0.10$; Feldman *et al.* 1987). Thus, our census results support Simpson's suggestions (1972, 1992) that southern Appalachian saw-whets are essentially birds of boreal and boreal-ecotone forests.

Saw-whets have, however, been reported from atypical sites in the southern Appalachians, including several observations meeting our operational definition of "territorial." Repeated observations of a singing male have been reported from a red-oak forest at 1,463 m (4,800 ft) near Pickens Nose in the Nantahala Mountains (Boynton, pers. comm.), and another has been reported from a northern hardwood forest at 1,524 m (5,000 ft) at Hooper Bald in the Unicoi Mountains (Hughes, pers. comm.). Two radio-harnassed saw-whets were monitored during the spring and summer of 1996[4] in a cool but low-elevation (1,036 m, 3,400 ft) drainage dominated by old-growth hemlock near the NPS Price Lake campground. None of these sites contained either spruce or fir. Moreover, 9 of the 159 responses to our census playbacks, representing owls on two territories, were from northern hardwood forests. Although one of these territories was in a mountain gap immediately surrounded by boreal forests, the other was in pure hardwood forest in the Great Balsam Mountains, a site at least 8 km (5 mi) from any appreciable stands of spruce or fir. Reproductive data would be needed to determine whether these atypical sites represent population "sources" or "sinks" (Bart and Forsman 1992, Pulliam 1988). These sites may, for example, represent sub-optimal habitat occupied by juvenile or subordinate birds that have been excluded from boreal habitats.

Whether saw-whets in these atypical sites are reproducing or not, two additional pieces of evidence suggest that such sites are rare. First, the data summarized in table 2 represent surveys by forest type immediately bordering our census routes. Because of the altitudinal zonation of forest types along our transects, however, we were in truth sampling multiple forest types even when our playback location was in spruce-fir. For example, we often heard responses from Barred Owls (*Strix varia* Barton) and Eastern Screech-owls (*Otus asio* Linnaeus) from the cove and oak-hickory forests in the valleys below, while saw-whets were never heard responding from below the mid-elevation northern hardwood zone. This is not, we believe, an artifact of species differences in song amplitude; the tooting call of saw-whets appears to carry at least as far as the bounce and whinny calls of screech owls. Moreover, our detection-threshold distance (Emlen 1984) for saw-whets was up to 1.2 km (0.75 mi), a distance sufficient for us to have noted the presence of saw-whets if they had responded from low-elevation forests.

Second, approximately one-dozen breeding-season surveys were conducted at two additional, high-elevation spruce-fir sites in 1991 and 1992: Mt. Rogers in southwestern Virginia and Grandfather Mountain in western North

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[4] Cooper, P.C. in prep. Winter ecology of southern Appalachian saw-whet owls. M.S. thesis in Biology, Appalachian State University, expected November 1998.

Carolina (fig. 2, unpubl. data from Tomlinson and Rowe). Surveys were conducted on foot, with playbacks approximately every 0.3 km (0.18 mi), alternately starting and finishing in high elevation spruce-fir stands (1,676 m or 5,500 ft on Mt. Rogers, 1,707 m or 5,600 ft on Grandfather Mountain) and low-elevation northern hardwood/oak-hickory forests (1,329 m or 4,360 ft on Mt. Rogers, 1,219 m or 4,000 ft on Grandfather Mountain). Territorial saw-whets were found on both mountains, always in either boreal or boreal-ecotone forests.

Densities Across Mountain Ranges

Of the 227 census hours, 66.25 were conducted in the Black Mountains in 1993 and 35.25 hours in 1994; 25.75 census hours were conducted in the Great Balsams in 1993, 32.25 in 1994; 51.0 hours were spent at Roan Mountain in 1993, with only 16.25 in 1994. None of the census hours from Roan in 1994 overlapped the peak calling season for saw-whets, and thus are dropped from further analyses.

Ten territories were mapped in the Great Balsams in 1993, eight in 1994 (fig. 3); seven were mapped in the Black Mountains in 1993, while five were found the following year; and finally, five territories were discovered on Roan in 1993. Reassuringly, Barb (1995), working independently of our project, also mapped five saw-whet territories on Roan in 1993.

The densities of territorial saw-whets differed across mountain ranges. Roan Mountain and the Great Balsam Mountains had similar densities in 1993, averaging one territory every 2.1 and 2.3 km (1.3 and 1.4 mi), respectively. Territories were slightly less dense in the Balsams in 1994, with one male per 3.1 km (1.9 mi). Densities in the Black Mountains were considerably lower than those in the other two study areas, with territories spaced every 3.9 and 4.5 km (2.4 and 2.8 mi) for 1993 and 1994, respectively.

DISCUSSION

Adelgid Impact on Saw-whet Density

Have saw-whet densities in the Great Balsam Mountains changed since Simpson's (1972) pioneering study of the late 1960's? Before answering, we should note the differences between our and Simpson's methodologies. Simpson whistled an imitation of the saw-whet's advertisement call; we broadcast taped calls at above-normal amplitudes. Simpson's surveys were conducted almost exclusively during the peak of saw-whet calling; our surveys started before, continued through, and ended after the peak season. And although Simpson's definition of what constitutes a saw-whet territory is basically the same employed here (i.e., an owl heard calling at the same site at least twice), Simpson pooled records over his 4 years of surveys while we required that an owl be heard twice during the same year. Nonetheless, densities reported by both studies are remarkably similar. We found 10 and eight territories in the Balsams in 1993 and 1994, respectively, while Simpson reported eight territories in both 1968 and 1969, with nine territories pooling over all 4 years of his study. The majority of Simpson's surveys were conducted in 1968 and 1969, and he reports an average density of one territory every 2.6 km (1.6 mi) for both years. By comparison, we found average densities in 1993-1994 of one territory per 2.7 km (1.7 mi). Similarities are also reported for calling sites (i.e., a location from which a saw-whet was heard at least once); 12 of the 15 calling sites reported by Simpson in the 1960's were occupied by saw-whets during our study in the 1990's.

Even though the Great Balsam Mountain range was the last range in the southern Appalachians to become infected with the woolly adelgid, the impact of these insects on the forests has been severe. Indeed, 84 percent of the fir have died, and mortality as a proportion of total fir volume is higher in the Balsams than in any other range (Dull *et al.* 1988). Comparisons of our results with Simpson's (1972) therefore suggest that adelgid-induced fir die-off has had little impact on the saw-whet population in the Great Balsam Mountains, and perhaps in the entire southern Appalachians. Telemetry data[5] do show that saw-whets avoid fir stands that have suffered heavy mortality. Apparently, the relatively healthy stands of red spruce just downslope of the degraded fir provide sufficient resources for the owls, as densities in the Great Balsams are

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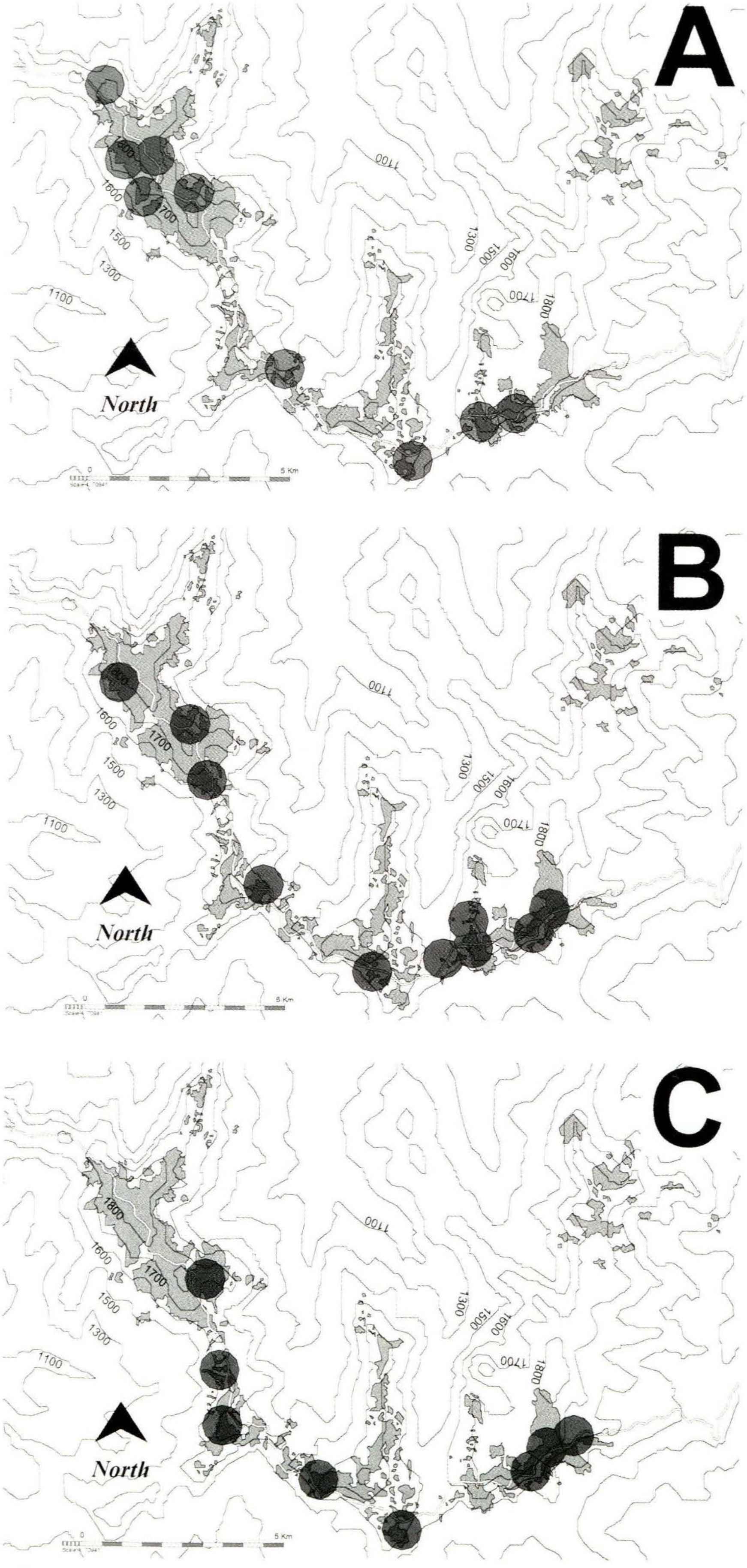
[5] Milling, T.C. in prep. Habitat requirements and population densities of saw-whets in the southern Appalachians. M.S. thesis in Biology, Appalachian State University, expected June 1998.


A
B
C
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1300
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5 Km

Figure 3.—*Locations of Northern Saw-whet Owl* (Aegolius acadicus) *calling clusters (territories) in the Great Balsam Mountains, North Carolina, during: (A) 1968-1971 (adapted from figure 1 in Simpson 1972); (B) 1993; and (C) 1994.*

essentially identical to those reported almost 30 years ago (Simpson 1972), prior to death of the fir. That the adelgid has had little impact on saw-whets is further supported by comparisons across mountain ranges. In our surveys, saw-whet densities were nearly identical on both Roan Mountain and in the Great Balsams, although adelgid-induced fir mortality is quite different on these peaks (44 vs. 84 percent, respectively; Dull *et al.* 1988). By contrast, saw-whet densities in the Black Mountains were twice as low, even though fir mortality (49 percent) is comparable to that on Roan (Dull *et al.* 1988). Explanations for differences in saw-whet densities across ranges are, at this point, speculative. Perhaps forests in the Black Mountains were damaged more severely by clearcutting earlier this century. Alternatively, prey abundance may have been higher during our survey years in the Great Balsams and on Roan than in the Blacks. Or perhaps the Black Mountains, being the highest range in the southern Appalachians, intercept more atmospheric pollutants and have reduced forest health. It may be noteworthy that the Black Mountains have the highest mortality of red spruce reported from any range in the southern Appalachians (Dull *et al.* 1988).

In the Great Balsam Mountains, at least, the population of Northern Saw-whet Owls appears relatively stable. Territorial densities and even calling sites look comparable from year-to-year and even decade-to-decade. We see little hint of the order-of-magnitude cycles reported for other populations of saw-whets (Palmer 1987, Swengel and Swengel 1995), although we caution that 2 consecutive years of surveys in the late 1960's and 2 in the mid-1990's may be insufficient for detecting such cycles. If confirmed, the stability of the southern Appalachian saw-whet population relative to other populations may be explained by dietary differences. Rodents comprise over 90 percent of the prey consumed by saw-whets at most sites (see review in Cannings 1993), and saw-whet populations may be tracking rodent cycles (Palmer 1987, Swengel and Swengel 1995).

Almost 60 percent of the prey consumed by saw-whets at our study sites, however, are shrews (Cockerel 1997). In North America, at least, shrew populations appear less cyclic than rodents (Getz 1989). Additionally, Korpimäki (1986) has demonstrated a significant, inverse relationship between owl-population cycles and dietary niche breadth in Tengmalm's Owls (*Aegolius funereus* Linnaeus); a broad diet presumably buffers certain Tengmalm's populations from the cycles of any single prey. Saw-whets in the southern Appalachians have a significantly higher dietary niche breadth than values reported for any other saw-whet population (Cockerel 1997), higher even than the most stable populations of Tengmalm's Owls. Two other trends reported by Korpimäki (1986) for Tengmalm's Owls also seem relevant: northern populations are more cyclic than southern populations; and nomadic/migatory populations are more cyclic than residents. Southern Appalachian saw-whets are, obviously, southern (fig. 1), and preliminary data suggest that these owls are year-round residents, exhibiting at most a moderate downslope movement only during harsh winter weather (Milling in prep., Cooper in prep.).

Southern Appalachian Saw-whet Owls: Current Status and Future Prospects

What is the size of the saw-whet population in the southern Appalachians? Based upon digital quantification of maps provided in Dull *et al.* (1988), we surveyed 734.4 ha (1,814.7 acres) of boreal and boreal-ecotone forest in the Great Balsam Mountains in 1993 and again in 1994. We found 10 saw-whets on territories in the surveyed area in 1993, suggesting a density of one pair per 73.4 ha (181.4 acres) of these forest types. This is the highest density of saw-whets we found at any site in either year. Similarly, we surveyed 1,252.5 ha (3,095 acres) of boreal and boreal-ecotone forest both years in the Black Mountains. We found only five territories in the Black Mountains in 1994, suggesting a density of one pair per 250.5 ha (619 acres) of spruce-fir and mixed spruce-fir-hardwood forest; this represents the lowest density of saw-whets in our study. Thus, saw-whets in the southern Appalachians utilize somewhere between 73.4 to 250.5 ha of boreal and boreal-ecotone forest in their territories.

How much boreal forest remains in the southern Appalachians? Using a restrictive definition of what constitutes "spruce-fir," Saunders (1979, cited in White *et al.* 1993) suggests that all that is left of this forest type is 69 km^2 (26.6

mi^2). Dull *et al.* (1988), using a broader definition that includes spruce-fir and ecotone forests, and perhaps pockets of northern hardwood (White *et al.* 1993), suggests there is 266 km^2 (102.7 mi^2) of boreal forest in the southern Appalachians.

Pessimistically, if saw-whets use 250.5 ha of boreal forest per pair and only 69 km^2 of this forest type remains, then there are only 27 pairs of saw-whets in the entire southern Appalachian population. More optimistically, if saw-whets use only 73.4 ha of boreal forest per territory, and 266 km^2 remains, then there are 362 pairs of saw-whets in the southern Appalachians. There are two reasons we feel the latter estimate is more reasonable. First, our survey work identified 22 territories (in 1993) at just three sites: Roan Mountain, the Great Balsam Mountains, and the Black Mountains. These three sites contain only 22 percent of the spruce-fir and ecotone forests in the entire southern Appalachian region (Dull *et al.* 1988), and we did not census all of the boreal forest found on just these three sites. Second, the operational definition employed by Dull *et al.* (1988) for what constitutes "spruce-fir" (including not just pure spruce-fir but mixed spruce-fir-northern hardwood ecotones and some inclusions of pure hardwood) is similar to what southern saw-whets appear to be choosing. Telemetry data (Milling in prep.) indicate that southern saw-whets typically include all of these forest types in their territories.

In 1994, however, a little over 12 percent of the territories we identified were in stands of almost pure northern hardwood (by contrast, no territories in 1993 were restricted to hardwoods). And as reviewed earlier, several saw-whets have been reported from other high-elevation hardwood forests and from cool, moist, lower-elevation sites dominated by mature hemlock. To account for birds that may be breeding in atypical habitat outside of the spruce and fir, it might be conservative to add an additional 20 percent to our estimate of 362 territories, producing a value of less than 450 pair. Using a correction factor of 40 percent, which we believe extravagant, still generates an estimate of only 500 pair of saw-whets in the southeastern U.S.

What will be the fate of this small, disjunct, and distinct population of saw-whets? Our data suggest that fir die-off has had little impact on southern saw-whets. Equally encouraging, allozyme analyses indicate that southern saw-whets still maintain relatively high levels of genetic heterozygosity (Tamashiro 1996). The future of this population, however, is far from secure. The small size and fragmented distribution of the population makes southern Appalachian saw-whets extremely vulnerable to stochastic environmental and demographic events (Lande 1988). Continued degradation of high-elevation forests could easily lead to the extirpation of saw-whets in the southeastern U.S., and the prognosis for these montane forests is disheartening (Boyce and Martin 1993, SAMAB 1996). A second exotic pest, the hemlock woolly adelgid (*Adelges tsugae* Annand), threatens to decimate eastern hemlocks (SAMAB 1996, Young *et al.* 1995), and acid deposition appears to be causing growth decline among red spruce (Thornton *et al.* 1994). Global warming may lead to the elimination of not only spruce and the remaining fir, but also northern hardwoods (Roberts 1989). Even if remnants of boreal forest do survive, increased ambient temperatures could push southern saw-whets beyond their own thermal tolerance limits (Brinker *et al.* 1997), leading to their eventual extirpation.

Surprisingly, outdoor recreation may also threaten the owls. Over 90 percent of the boreal forests of the southern Appalachians are held in public ownership (Boyce and Martin 1993), primarily as national forests or national parks, including Great Smoky Mountains National Park and the Blue Ridge Parkway. Two radio-harnessed saw-whets, one each at two different campgrounds along the Parkway, abandoned their territories when these seasonal campgrounds opened in the spring (Milling in prep., Cooper in prep.). Additionally, heavily used hiking trails (e.g., the Appalachian Trail and the Cloudland Trail on Roan Mountain), appear to have below-normal densities of saw-whets (Milling in prep.). Between 1960 and 1990, the human population of the states of North Carolina, Tennessee, and Virginia increased by over 46 percent (Boyce and Martin 1993). Recreational use of the high-elevation forests appears to be growing even faster; trail use by day hikers in Great Smoky Mountains National Park increased by 57 percent between 1979 and 1993 alone (Anonymous 1995), and visits to the area's national forests almost doubled during this period (figure 4.21 in SAMAB 1996 vol. 4). The demand for additional campgrounds, picnic areas, and scenic roadways will continue to grow (SAMAB 1996), with potentially adverse effects on the saw-whet population.

What then can be done? First, we call on state wildlife agencies in North Carolina, Tennessee, and Virginia to add southern Appalachian saw-whets to their respective state's endangered species lists; currently, saw-whets are listed only as a "species of special concern" in each of these three states. Second, long-term monitoring should be initiated to assess trends in the southern Appalachian saw-whet population; such monitoring could employ a combination of systematic playback surveys and the use of nest boxes (Hayward *et al.* 1992). Lastly and most importantly, greater attention needs to be directed at protecting the high-elevation boreal forests of the southern Appalachians, recently recognized as the second-most endangered ecosystem in the U.S. (Noss and Peters 1995). Closing on a brighter note, we mention that at least two different public opinion polls demonstrate overwhelming support by people in the southern Appalachians for protecting the region's biological diversity (SAMAB 1996, Williams and Gaskill 1996). We hope that southern Appalachian saw-whets receive this protection.

ACKNOWLEDGMENTS

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LITERATURE CITED

Alsop, F.J. III. 1991. Birds of the Smokies. Gatlinburg, TN: Great Smoky Mountains Natural History Association. 167 p.

Anonymous. 1995. A strategic plan for managing backcountry recreation in Great Smoky Mountains National Park. Gatlinburg, TN: Great Smoky Mountains National Park. 155 p.

Barb, M.A. 1995. Natural history of the Northern Saw-whet Owl *(Aegolius acadicus)* in the southern Appalachian mountains. Johnson City, TN: East Tennessee State University. 68 p. M.S. thesis.

Bart, J.; Forsman, E.D. 1992. Dependence of Northern Spotted Owls (*Strix occidentalis caurina*) on old-growth forest in the western USA. Biological Conservation. 62: 95-100.

Boyce, S.G.; Martin, W.H. 1993. The future of the terrestrial communities of the southeastern United States. In: Martin, W.H.; Boyce, S.G.; Echternacht, A.C., eds. Biodiversity of the southeastern United States, Vol. 2: Upland terrestrial communities. New York, NY: John Wiley & Sons, Inc.: 339-366

Busing, R.T.; Clebsch, E.E.C.; Eagar, C.C.; Pauley, E.F. 1988. Two decades of change in a Great Smoky Mountains spruce-fir forest. Bulletin of the Torrey Botanical Club. 115: 25-31.

Cannings, R.J. 1993. Northern Saw-whet Owl *(Aegolius acadicus).* In: Poole, A.; Gill, F., eds. The Birds of North America, no. 42. Philadelphia, PA: Academy of Natural Sciences, and Washington, DC: the American Ornithologists' Union: 1-20.

Cockerel, B.E., Jr. 1997. Prey selection of the Nothern Saw-whet Owl (*Aegolius acadicus*) in the southern Appalachian Mountains. Boone, NC: Appalachian State University. 91 p. MS thesis.

Crutchfield, P.J. 1990. Northern Saw-whet Owl. In: Lee, D.S.; Parnell, J.F., eds. Endangered, threatened, and rare fauna of North Carolina. Part III. A re-evaluation of the birds. Occasional Papers of the North Carolina Biological Survey 1990-91: 34-36.

Delcourt, H.R.; Delcourt, P.A. 1984. Late-quaternary history of the spruce-fir ecosystem in the southern Appalachian mountain region. In: White, P.S., ed. The southern Appalachian spruce-fir ecosystem: its biology and threats. National Park Service Research/Resources Management Report SER-71: 22-35.

Dull, C.W.; Ward, J.D.; Brown, H.D.; Ryan, G.W.; Clerke, W.H.; Uhler, R.J. 1988. Evaluation of spruce and fir mortality in the southern Appalachian mountains. Protect. Rep. R8-PR. U.S. Department of Agrculture. 92 p.

Emlen, J.T. 1984. An observer-specific, full-season, strip-map method for censusing songbird communities. Auk. 101: 730-740.

Feldman, D.S., Jr.; Hofmann, R.; Gagnon, J.; Simpson, J. 1987. StatView II: The solution for data analysis and presentation graphics. Berkeley, CA: Abacus Concepts, Inc. 278 p.

Fuller, M.R.; Mosher, J.A. 1981. Methods of detecting and counting raptors: a review. Studies in Avian Biology. 6: 235-246.

Getz, L.L. 1989. A 14-year study of *Blarina brevicauda* populations in east-central Illinois. Journal of Mammalogy. 70: 58-66.

Groth, J.G. 1988. Resolution of cryptic species in Appalachian Red Crossbills. Condor. 90(4): 745-760.

Gross, D.A. 1992. Northern Saw-whet Owl. In: Brauning, D.W., ed. Atlas of breeding birds in Pennsylvania. Pittsburgh, PA: University of Pittsburgh Press: 166-167.

Hayward, G.D.; Steinhorst, R.K.; Hayward, P.H. 1992. Monitoring Boreal Owl populations with nest boxes: sample size and cost. Journal of Wildlife Management. 56: 777-785.

Hill, C.E. 1995. The vocal behavior of Northern Saw-whet Owls: an analysis of context and variation. Richmond, KY: Eastern Kentucky University. 52 p. M.S. thesis.

Johnsgard, P.A. 1988. North American owls: biology and natural history. Washington, DC: Smithsonian Institution Press. 295 p.

Johnson, R.R.; Brown, B.T.; Haight, L.T.; Simpson, J.M. 1981. Playback recordings as a special avian censusing technique. Studies in Avian Biology. 6: 68-75.

Korpimäki, E. 1986. Gradients in population fluctuations of Tengmalm's Owl *Aegolius funereus* in Europe. Oecologia. 69: 195-201.

Korstian, C.F. 1937. Perpetuation of spruce on cut-over and burned lands in the higher Appalachian mountains. Ecological Monographs. 7: 125-167.

Lande, R. 1988. Genetics and demography in biological conservation. Science. 241: 1455-1460.

Noss, R.F.; Peters, R.L. 1995. Endangered ecosystems: a status report on America's vanishing habitat and wildlife. Washington, DC: Defenders of Wildlife. 132 p.

Otter, K. 1996. Individual variation in the advertising call of male Northern Saw-whet Owls. Journal of Field Ornithology. 67: 398-405.

Palmer, D.A. 1987. Annual, seasonal, and nightly variation in calling activity of Boreal and Northern Saw-whet Owls. In: Nero, R.W.; Clark, R.J.; Knapton, R.J.; Hamre, R.H., eds. Biology and conservation of northern forest owls: symposium proceedings; 1987 February 3-7; Winnipeg, MB. Gen. Tech. Rep. RM-142. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 162-168.

Parmalee, P.W.; Klippel, W.E. 1982. Evidence of a boreal avifauna in middle Tennessee during the late Pleistocene. Auk. 99: 365-368.

Pulliam, H.R. 1988. Sources, sinks, and population regulation. American Naturalist. 132: 652-661.

Rabenold, K. 1984. Birds of Appalachian spruce-fir forests: dynamics of habitat-island communities. In: White, P.S., ed. The southern Appalachian spruce-fir ecosystem: its biology and threats. National Park Service Research/Resources Management Report SER-71: 168-186.

Roberts, L. 1989. How fast can trees migrate? Science. 243: 735-737.

SAMAB. 1996. The Southern Appalachian Assessment. Vol. 1: Summary Report, 118 p. Vol. 4: Social/Cultural/Economic Technical Report, 219 p. Vol 5: Terrestrial Technical Report, 286 p. U.S. Department of Agriculture, Forest Service, Southern Region.

Saunders, P.F. 1979. The vegetational impact of human disturbance on the spruce-fir forests of the southern Appalachians. Durham, NC: Duke University. Ph.D. dissertation.

Simpson, M.B., Jr. 1972. The Saw-whet Owl population of North Carolina's southern Great Balsam Mountains. Chat. 36: 39-47.

Simpson, M.B., Jr. 1992. Birds of the Blue Ridge Mountains. Chapel Hill, NC: University of North Carolina Press. 354 p.

Stupka, A. 1963. Notes on the birds of Great Smoky Mountains National Park. Knoxville, TN: University of Tennessee Press. 242 p.

Swengel, A.B.; Swengel, S.R. 1995. Possible four-year cycle in amount of calling by Northern Saw-whet Owls. Passenger Pigeon. 57: 149-155.

Swengel, S.R.; Swengel, A.B. 1987. Study of a Northern Saw-whet Owl population in Sauk County, Wisconsin. In: Nero, R.W.; Clark, R.J.; Knapton, R.J.; Hamre, R.H., eds. Biology and conservation of northern forest owls: symposium proceedings; 1987 February 3-7; Winnipeg, MB. Gen. Tech. Rep. RM-142. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 199-208.

Tamashiro, D.A. 1996. Genetic and morphological variation in northern saw-whet populations in eastern North America. Boone, NC: Appalachian State University. 112 p. M.S. thesis.

Thornton, F.C.; Joslin, J.D.; Pier, P.A.; Neufeld, H.; Seiler, J.R.; Hutcherson, J.D. 1994. Cloudwater and ozone effects upon high elevation red spruce: a summary of study results from Whitetop Mountain, Virginia. Journal of Environmental Quality. 23: 1158-1167.

White, P.S.; Buckner, E.R.; Pittillo, J.D.; Cogbill, C.V. 1993. High-elevation forests: spruce-fir forests, northern hardwoods forests, and associated communities. In: Martin, W.H.; Boyce, S.G.; Echternacht, A.C., eds. Biodiversity of the southeastern United States, Vol. 2: Upland terrestrial communities. New York, NY: John Wiley & Sons, Inc.: 305-337.

Williams, W.; Gaskill, P. 1996. Profile of recreation users at Roan Mountain. Spec. Rep. Burnsville, NC: U.S. Department of Agriculture, Forest Service, Toecane Ranger District, Pisgah National Forest. 63 p.

Wright, H.E., Jr. 1981. Vegetation east of the Rocky Mountains 18,000 years ago. Quatenary Research. 15: 113-125.

Young, R.F.; Shields, K.S.; Perlyn, G.P. 1995. Hemlock woolly adelgid (Homoptera: Adelgidae): stylet bundle insertion and feeding stations. Annals of the Entomological Society of America. 88: 827-835.

Importance of Prairie Wetlands and Avian Prey to Breeding Great Horned Owls (*Bubo virginianus*) in Northwestern North Dakota

Robert K. Murphy[1]

Abstract.—Prey use by Great Horned Owls (*Bubo virginianus*) is documented widely in North America, but not in the vast northern Great Plains. During spring through early summer 1986-1987, I recorded 2,900 prey items at 22 Great Horned Owl nesting areas in the prairie pothole farm- and rangelands of northwestern North Dakota. The owls relied heavily on wetland-dependent prey species (overall, 57 percent by number and 76 percent biomass) especially ducks (Anserinae) and rails (Rallidae). Far more avian (65 percent by number and 84 percent biomass) and less mammalian prey were used than typically reported. Variation in diet composition among owl families was not explained well by nesting area habitat, and was dominated by prey from wetlands regardless of wetland habitat availability.

Diets of Great Horned Owls (*Bubo virginianus*) are better documented than those of most other North American strigiforms. The owl preys mainly on small to mid-size mammals especially small rodents and leporids (Errington *et al.* 1940; Korschgen and Stuart 1972; McInvaille and Keith 1974; Marti and Kochert 1995, 1996; Voous 1988) although its list of prey includes diverse sizes and taxa (see Bent 1938). Despite broad knowledge of the Great Horned Owl's diet, little is known of its prey use in the vast northern Great Plains of midcontinent North America. Numerous studies of Great Horned Owl diets have been conducted in more wooded habitats of nearby Great Lakes States (Errington *et al.* 1940, Orians and Kuhlman 1956, Petersen 1979) and the boreal forest ecotone (McInvaille and Keith 1974, Rusch *et al.* 1972), but implications for predator-prey relationships in the Great Plains are only speculative.

Abundance and distribution of Great Horned Owls have increased in the northern Great Plains since the region was settled by Europeans about a century ago, due to increases in woodland breeding habitat associated with tree-planting and suppression of prairie fires (Murphy 1993, Sargeant *et al.* 1993). The increase in this generalist predator may have implications for population dynamics of species on which it preys. My objectives were to quantify diet composition of breeding Great Horned Owls in an area of mixed farm- and rangeland in the northern Great Plains, to assess variation in prey use among owl pairs, and to test whether such variation is explained by habitat makeup around nests.

STUDY AREA

Diets of nesting Great Horned Owls were examined during May to early July, 1986 and 1987 on 93 km^2 Lucy Township and about 100 km^2 of adjacent similar habitat and land use in Burke County, northwestern North Dakota (48°40'N; 102°35'W). The study area was within a rolling to hilly glacial moraine known as the Missouri Coteau (Bluemle 1977). Climate was semi-arid with cold winters and warm summers. Annual precipitation was 46 cm in 1986 and 31 cm in 1987 compared to a 42-cm average, and water levels in local wetlands were average and below average in respective years (Murphy 1993:155). Land use was a mix of grain farming and cattle ranching. Habitat composition on Lucy Township was 41 percent native (*Stipa-Agropyron*) prairie (about one-half grazed heavily by domestic livestock and one-half grazed lightly or idle) with scattered tall shrubs such as hawthorn (*Crateagus chrysocarpa*) or chokecherry (*Prunus virginiana*); 31

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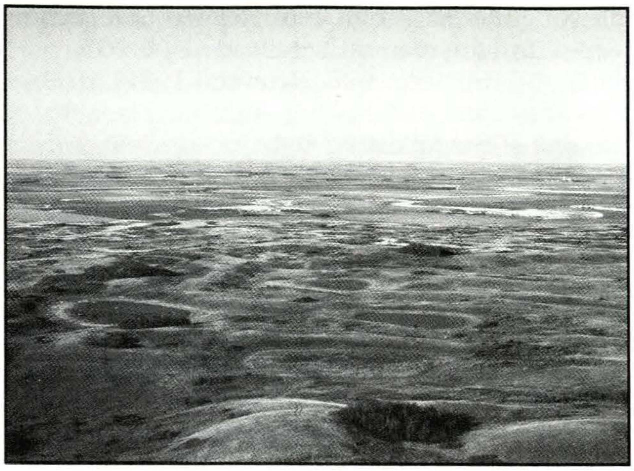

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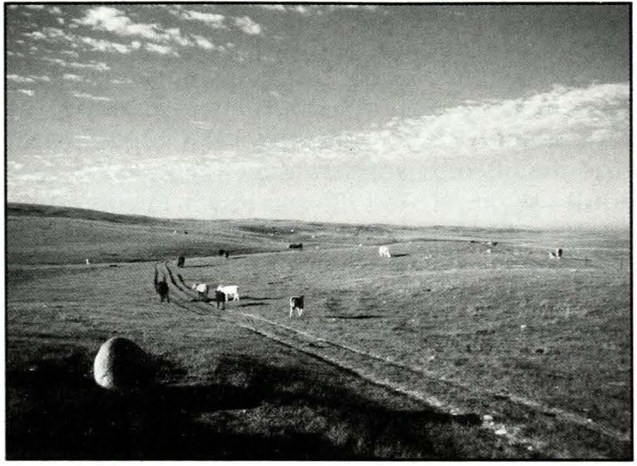
The study area was on the Missouri Coteau, a glacial moraine dotted with wetlands known as prairie potholes. Land use was a mix of grain farming and cattle ranching.

percent cropland, one-third of which annually was fallow; 19 percent seasonal, semi-permanent, and permanent wetlands (classification according to Stewart and Kantrud [1971]); 5 percent tame grass-alfalfa hay; 2 percent small (< 1 ha), scattered clumps of quaking aspen (*Populus tremuloides*) trees (mean = 4.7 clumps/km^2, SD = 3.4); and 2 percent roads, farmsteads, and shelterbelts. The area was sparsely inhabited by humans (one farmstead/8 km^2).

Raptors that nested commonly on the study area included Red-tailed Hawk (*Buteo jamaicensis*) (0.16 occupied nests/km^2), Swainson's Hawk (*B. swainsoni*) (0.08/km^2), Northern Harrier (*Circus cyaneus*) (> 0.2/km^2), and Great Horned Owl (0.11/km^2) (Murphy 1993). Great Horned Owls occurred year-round and nesting pairs hatched their eggs in early to mid-April.

METHODS

Each spring I systematically searched 80 km^2 of Lucy Township (access was denied on 13 km^2) for occupied nests of raptors (Murphy 1993) and subsequently monitored prey use by all successful Great Horned Owl pairs (those that produced nestlings at least 3 weeks old). I augmented this sample of owl diets with like data from all successful Great Horned Owl nests on similar land use and habitat within the Missouri Coteau, up to 10 km north, south, and east of Lucy Township.



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Mixed grass prairie made up 41 percent of the study area. About one-half of this was grazed heavily each year by cattle, and the rest was grazed lightly or not at all. When ungrazed, average heights of the prairie vegetation reached about 10 cm on hilltops to 40 cm near wetland edges.

Diet

In May, when owlets were 4 weeks old, I tethered them on platforms that were about 2 m above ground in sheltered sites < 9 m from nests (Petersen and Keir 1976). I subsequently visited the platforms every 3-4 days between 1000-2000 hours for 6-8 weeks after which young were released. During each visit I weighed owlets and collected all regurgitated pellets and discarded (inedible) prey remains. Fresh (edible) prey were identified, marked by cutting off a foot. I used standard techniques to analyze pellets (Marti 1987). I avoided duplicating the count of any prey item by conservatively choosing the lowest number of items represented collectively by pellets, discarded remains, and fresh items, including fresh items noted at the previous visit (Collopy 1983, Craighead and Craighead 1956, Marti 1987).

Mean weights of prey were obtained from specimens collected on the study area (Appendix 5 in Murphy [1993]) and from published literature (Dunning 1984, James and Seabloom 1969, Jones *et al.* 1983). For weights of prey represented by remains in owl pellets, I relied mainly on measurement of skeletal elements such as passeriform synsacra and tarsometatarsi (tarsi) to estimate approximate size and age of prey (Marti 1987). Ossification of major skeletal elements and (for birds) presence of down versus emerging or fully developed contour feathers also were helpful in approximating age and size of prey in pellets. Weights were assigned to juvenile prey relative to those of adults of same species: (1) large juvenile (adult weight x 0.75), (2) two-thirds grown (adult weight x 0.66), and (3) one-half grown (0.5 x adult weight). For prey of undetermined age, I used prey observed at tether platforms as a reference and assigned the average weight of conspecific prey for which age could be determined. Weights of undetermined species of juvenile ducks were estimated by comparing tarsus lengths to a composite age-growth curve weighted according to relative abundance of small, medium, and large species among duckling prey of known identity that were observed on platforms (Murphy 1993:196). I assigned each invertebrate prey (e.g., Orthoptera) a weight of 1 g.

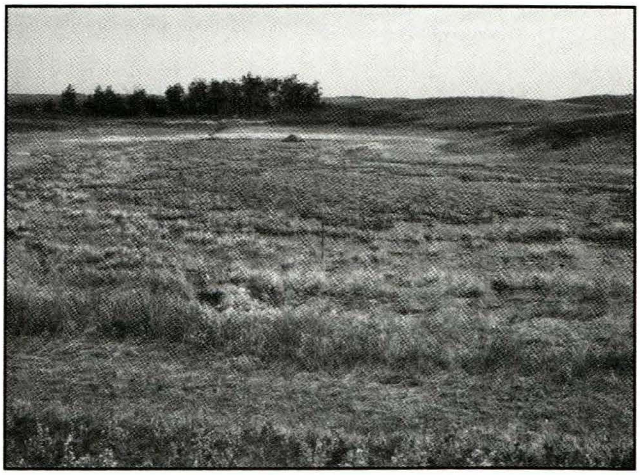
I report dietary makeup in terms of relative (percentage) frequency and biomass. Percentage frequency (i.e., the proportion by numbers) was calculated by dividing the number of individuals of each prey category by the total number of prey items observed. Percentage biomass was estimated by multiplying the number of individuals of each prey category by their respective mean weight, then dividing the subtotal of each prey category by the grand total prey weight (Marti 1987). For each prey category that comprised > 5 percent (frequency) of prey pooled from all owl tether platforms, I estimated the average biomass in g of prey killed daily by each Great Horned Owl pair. I refer to this estimate as a daily biomass consumption rate (DBC). DBC (g/day) was determined for a given owl family by multiplying the percentage biomass of each prey category times daily food needs (total g) of adults and young combined (Craighead and Craighead 1956:312). I assumed that composition of prey consumed by adults was the same as that delivered to owlets, and that each adult and juvenile Great Horned Owl required about 144 g of prey daily (McInvaille and Keith 1974). Last, I calculated food-niche breadth at a coarse level, using Levins' formula: $1/\Sigma\ p_i^2$, where p_is were frequency proportions of each prey class (Marti 1987).

Habitat Variables

I defined nesting area as the area within a 1 km radius of a tether platform and assumed this roughly defined a Great Horned Owl home range (Craighead and Craighead 1956:257, Marti and Kochert 1996, Petersen 1979). Habitat within each owl nesting area was classified into one of the following eight categories: aspen tree clump, seasonal wetland, semi-permanent wetland, cropland, hayland (tame hay), pasture (moderately to heavily grazed native prairie), idle prairie (rested > 2 years), and miscellaneous (farmstead, road right-of-way); the proportion (percentage) of a nesting area that each habitat comprised was determined from area measurement on aerial photographs (1:15,840). Within each nesting area I also measured area (ha) of each of the eight habitats that was within 100 m of a perch > 6 m high because Great Horned Owls typically hunt from elevated perches (e.g., Petersen 1979). I also measured distance (m) from tether platform to nearest patch for each of the eight habitats (hereafter I refer to these simply as e.g., proximity or distance to cropland). Thus, at every owl nesting area there was a total of 24 habitat variables measured.

Statistical Treatment of Data

Null hypotheses regarding Great Horned Owl diets and relationships between diet and habitat were tested by ANOVA and contingency tests (Sokal and Rohlf 1981). Data sets were tested for homogeneity of variances using F-test procedures in BMDP (Dixon 1983). Hypotheses of no overall, between-year difference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Prairie wetlands made up 19 percent of the area and were diverse in size and type (water permanency). Clumps of quaking aspen trees were widely scattered and typically occurred on wetland edges.

in frequency proportions of prey used by Great Horned Owls were tested by using the mulivariate analysis of covariance procedure in SAS (SAS Institute 1989). Univariate analyses of covariance were used if overall year effect was significant in the multivariate test. I convey exact probability levels for test results where $P > 0.001$ and consider $P < 0.05$ to be grounds for rejecting null hypotheses.

Linear regression models (Neter *et al.* 1985) were used to try to explain variation in use of important prey types among Great Horned Owl families (i.e., nesting areas). Either percentage biomass or DBC for each respective nesting area was entered as the dependent variable. I used biomass in this analysis because it may better convey relative importance of prey to raptors than frequency (Marti 1987, Rusch *et al.* 1972). The database randomly excluded data from 1 year for individual nesting areas monitored both in 1986 and 1987. All 24 habitat variables were candidates as independent (explanatory) variables in regressions. Also, abundance indices for prey used by owls in significantly different frequency proportions between years were derived from local surveys by the U.S. Fish and Wildlife Service (Murphy 1993), and were added as independent variables to account for year effect. I included number of tethered young as an independent variable when DBC was the dependent variable. The stepwise regression procedure in BMDP (Dixon 1983) was used to select five to eight potentially best independent variables. Then all possible one-, two-, and three-variable models were explored. Independent variables not normally distributed were log transformed. I checked for multicollinearity among independent variables by using correlation and examined residual plots for the assumption of constant variance. Standardized regression coefficients and associated P-values (probability of t in reduced model test for coefficient) were reported to convey relative importance and validity of independent variables in multivariate models. I accepted models for which F for the regression fit had an associated probability of $P < 0.05$.

RESULTS

I recorded 1,200 prey items at 12 Great Horned Owl tether platforms during 628 platform-days (i.e., a site monitored 1 day) in 1986 and 1,700 items at 12 tether platforms during 683 platform-days in 1987. Twenty-two different nesting areas were represented in this sample; two nesting areas were sampled both years. One to three owlets were tethered on each platform (means, 1.8 and 2.3 young/platform in 1986 and 1987, respectively). None of 49 tethered owlets died on platforms; all gained or maintained weight without need for supplemental feeding (Petersen and Keir 1976). Evidence of surplus prey on platforms was rare, however. Owlets were released while still being fed at a relatively constant rate by tending adults.

Overall Diet

Birds comprised most prey delivered especially in terms of overall biomass (subtotals, table 1); > 47 species were represented (all prey recorded, including scientific names, are listed in Appendix A). Mammals were far less important, particularly in biomass contribution. Other prey classes were insignificant (< 2 percent frequency and 1 percent biomass in aggregate, table 1). Mean prey mass was 196.6 g (range < 1 to 1,250 g, N = 2,900), and overall dietary diversity (food niche breadth) was 1.88 (N = five prey classes).

Ducks (10 species; 77 percent juveniles) were the most important prey category (table 1). Rails, especially American Coot (nearly all adults; 70 percent frequency, 94 percent biomass of rallid prey), were the second most important prey. Voles (mainly meadow vole), mice (mainly deer mouse), and passeriforms (mostly juvenile blackbirds) each contributed > 10 percent frequency of prey and, along with

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Great Horned Owls nested in aspen, usually in old Buteo *spp. nests.*

Table 1.—*Percentage composition of prey used by nesting Great Horned Owls (*Bubo virginianus*) in the Missouri Coteau of northwestern North Dakota during May to early July, 1986 and 1987, based on prey items pooled from all owl families.*[1]

Prey category[2]	Frequency N	Frequency Percent	Biomass kg	Biomass Percent	Percentage of nesting areas where preyed on[3]
Mammals					
White-tailed jackrabbit	95	3.3	43.0	7.5	63.6
Ground squirrel	42	1.4	10.1	1.8	81.8
Mouse	385	13.3	6.4	1.1	100.0
Vole	328	11.3	9.7	1.7	100.0
Muskrat	20	0.7	9.5	1.7	36.4
Norway rat	87	3.0	17.7	3.1	45.5
Miscellaneous	14	0.5	1.4	0.2	—
Subtotal		33.5		17.1	
Birds					
Grebe	99	3.4	35.4	6.2	95.5
Duck	1,010	34.8	256.5	45.0	100.0
Grouse and partridge	34	1.2	17.4	3.1	54.5
Rail	315	10.9	117.1	20.5	100.0
Shorebird	79	2.7	7.6	1.3	90.9
Passeriform	303	10.4	17.2	3.0	100.0
Domestic chicken	20	0.7	15.5	2.7	4.5
Miscellaneous	18	0.6	3.6	0.6	—
Subtotal		64.7		82.4	
Amphibian	38	1.3	1.9	0.4	50.0
Reptile	1	< 0.1	0.1	< 0.1	4.5
Insect	12	0.4	< 0.1	< 0.1	31.8
Total	2,900	100.0	570.1	100.0	

[1] Total of 12 and 12 nesting areas monitored in 1986 and 1987; two nesting areas were monitored both years.

[2] See Appendix A for names of prey species not specifically identified in table.

[3] Proportion of 22 nesting areas at which a given species or species group occurred as prey at least once during 1986-1987.

rails and ducks, were used by all owl families. White-tailed jackrabbits (all juveniles) and grebes (nearly all adults) contributed > 5 percent of overall biomass although jackrabbit prey was not used at many nesting areas. In contrast, shorebird and ground squirrel prey were used widely but infrequently by any one owl family and contributed little to biomass. One owl family switched from a diverse diet of wild prey to almost exclusively domestic chickens and Norway rats (means, 0.7 chickens and 1.2 rats found daily on the tether platform with three owlets) after 250 half-grown cockerels were released into an open pen lacking roosting shelter at a farmstead 0.5 km away. Galliform prey, composed equally of Sharp-tailed Grouse and Gray Partridge (nearly all adults), were used infrequently and by only about one-half of owl families. Tiger salamanders comprised nearly all amphibian prey; 46 percent were noted at a single tether platform.

Wetlands comprised 19 percent of habitat on Lucy Township and adjacent lands and averaged the same proportion of habitat in Great Horned Owl nesting areas, but wetland-dependent prey comprised 57 percent frequency and 76 percent biomass of prey in owl diets (pooled data, compared to 19 percent wetland composition; chi-square goodness-of-fit, both P < 0.001). These prey were ducks, rails, grebes, certain passeriforms (Yellow-headed Blackbird, Red-winged Blackbird) and shorebirds (e.g., Black Tern), muskrats, and tiger salamanders.

Variation in Diet

Year Effect

There was a difference between years in overall use (percentage frequency) of voles, mice, and passeriforms (table 2). The relative frequency of voles as prey was greater in 1987 when voles were more abundant in northwestern North Dakota (1986-1987 abundance indices: 0.1 and 12.4 captures/100 snap-trap nights [Murphy 1993]). Less significant was the decrease in frequency of mouse and passeriform prey from 1986 to 1987. Frequency of rallid prey appeared greater in 1987, but the difference was not significant (P = 0.142). Use of duck prey did not differ between years, even though duck abundance locally was below average in 1986 and about average in 1987 (May abundance indices: 54 and 104 ducks/km^2), a trend opposite that of local wetland conditions (Murphy 1993:155).

Variation Among Nesting Areas

I observed marked variability in use of prey among Great Horned Owl nesting areas (table 2). For example, percentage of dietary biomass represented by ducks ranged 28-90 percent in 1986. Habitat also varied among nesting areas (table 3), but was not dissimilar between

Table 2.—*Variation in relative diet composition*[1] *of Great Horned Owls (*Bubo virginianus*) between 1986 and 1987, and among nesting areas*[2] *within years, northwestern North Dakota.*

	Percentage frequency						Percentage biomass					
	1986			1987			1986			1987		
Prey category	**Mean**	**(SD)**	**Range**	**Mean**	**(SD)**	**Range**	**Mean**	**(SD)**	**Range**	**Mean**	**(SD)**	**Range**
Mammals												
White-tailed jackrabbit	5.0	(3.7)	0-9.8	1.9	(2.5)	0-7.8	10.8	(9.5)	0-31.8	4.8	(6.4)	0-18.6
Ground squirrel	2.0	(2.5)	0-9.0	1.0	(0.7)	0-3.0	2.1	(2.6)	0-9.3	1.5	(1.6)	0-5.8
Mouse[3]	18.1	(9.4)	4.9-38.1	11.4	(6.7)	3.7-23.9	1.7	(1.1)	0.6-4.0	1.0	(0.6)	0.3-2.2
Vole[3]	7.0	(4.3)	1.9-14.3	14.3	(2.8)	9.0-20.2	1.0	(0.6)	0.3-1.9	2.2	(0.7)	1.3-3.7
Birds												
Grebe	3.2	(2.3)	0-7.4	2.9	(1.7)	0.7-5.4	5.7	(4.0)	0-12.7	5.5	(3.2)	1.1-11.2
Duck	35.5	(15.7)	16.7-71.3	32.5	(12.1)	8.5-59.3	51.4	(18.3)	27.8-90.2	42.3	(12.2)	17.0-66.9
Grouse and Partridge	1.3	(3.3)	0-11.4	1.2	(1.0)	0-3.1	2.3	(5.9)	0-20.9	3.4	(2.6)	0-8.8
Rail	7.6	(5.3)	0.8-19.6	14.4	(7.8)	6.3-32.2	15.9	(11.4)	0.4-42.0	25.7	(9.2)	8.7-36.5
Shorebird	3.2	(2.4)	0-7.1	2.4	(3.0)	0-10.9	1.6	(1.1)	0-4.0	1.2	(1.3)	0-4.7
Passeriform[3]	12.1	(5.1)	4.1-19.4	9.0	(4.4)	3.5-15.5	3.2	(1.8)	0.9-7.0	2.9	(2.0)	0.4-6.9
Amphibians	1.9	(3.9)	0-13.9	0.6	(0.7)	0-2.0	0.6	(1.3)	0-4.7	0.2	(0.2)	0-0.6
Between-year difference, overall diet				P = 0.006[4]						P > 0.05		

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[1] Excludes prey or prey groups that comprised < 1 percent dietary composition by frequency during 1986-1987.

[2] Based on 22 separate nesting areas monitored: N = 11 in 1986 and N = 11 in 1987.

[3] Significant difference in relative (percentage) frequency composition between years; univariate analysis of covariance: mouse, P = 0.019; vole, P = 0.005; passeriform, P = 0.047.

[4] Significant difference in overall relative (percentage) frequency between years; multivariate analysis of covariance: Wilks' lambda = 0.014, F = 18.06, df = 16.

Table 3.—*Composition of seven major habitat types among 22 Great Horned Owl (*Bubo virginianus*) nesting areas, northwestern North Dakota, 1986-1987.*

Habitat type	Percentage of area within 1 km of nest Mean	SD	Range
Quaking aspen tree clump	3.2	2.4	0.8-8.7
Seasonal wetland	10.1	4.6	2.3-19.8
Semi-permanent wetland	8.1	5.9	0.5-24.0
Cropland	28.4	15.4	3.1-56.7
Hayland	4.6	6.4	0-29.8
Pasture	22.8	14.4	1.9-55.5
Idle prairie	20.1	14.3	0.0-45.1

nesting areas on (N = 8) compared to off (N = 14) Lucy Township except semipermanent wetlands were slightly more prevalent on the township (means, 11 versus 7 percent; df = 21, F = 6.6, P = 0.022). Dietary diversity (food niche breadth, class level) ranged 1.38-2.07 among nesting areas (mean = 1.81, SD = 0.21, N = 22), and wetland-dependent prey species contributed up to 95.8 percent of dietary biomass (mean = 77.6, SD = 15.5). Next I present models for predicting use of prey categories that comprised > 5 percent overall frequency in table 1 except passeriforms (no models suitably explained variation in passeriform use), and for wetland-dependent prey collectively.

Mice and voles.—No models suitably accounted for variation in use of mouse prey among Great Horned Owl nesting areas. Use of mice in terms of mean biomass consumed daily (DBC) was weakly explained by percentage cropland in nesting areas ($R^2 = 0.142$, F = 3.31, P = 0.084). For voles, hayland was a common although not strong predictor of owl predation in multiple variable models (table 4), and alone it was nonsignificant (e.g., percentage hayland [log]: $R^2 = 0.135$, F = 3.31, P = 0.093). The functional response to changed vole abundance during 1986-1987 was indicated by a year-effect variable. Variation also was partly explained by the number of young owls being fed, a variable unimportant in models for other prey.

Rails.—Almost no suitable models were produced for rallids. Owls appeared to consume less rail biomass (nearly all represented by American Coot) as the amount of idle prairie near perches increased in nesting areas (table 4).

Ducks.—Models with relative biomass as the dependent variable inadequately explained variation in use of duck prey among owl nesting areas. However, nearly one-half of the variation in DBC of ducks was explained by pasture and distance to nearest road or farmstead (table 4). Owls consumed more duck prey when there was more pasture in nesting areas or when pasture was closer to nests, and less as roads and farmsteads became closer. I expected that main components of breeding duck habitat, wetlands and idle prairie (i.e., nesting cover), might explain most variation in use of duck prey among Great Horned Owl nesting areas, yet these variables were unimportant (e.g., percentage semi-permanent wetland in nesting area: $R^2 = 0.004$, df = 21, F = 0.08, P = 0.775).

Next I examined use of adult and juvenile duck prey separately (table 4). In the only model marginally suitable for adult ducks, extent of pasture and aspen tree clumps explained more than one-third of DBC variation. Duckling DBC did not relate to differences in pasture among owl nesting areas, and extent of semi-permanent wetland was a marginally significant predictor. From this second analysis, I conclude the positive relationship of pasture to overall use of duck prey (models I and II in table 4) pertained mostly to adult ducks.

Wetland-dependent Prey.—Perhaps use of either duck or rail prey was poorly explained by proximity or prevalance of wetlands because some owl families relied more on alternative wetland-dependent prey. If so, total wetland-dependent prey use should have reflected wetland availability if prey resources were used in proportion to their respective habitats in owl nesting areas. Distance to nearest semi-permanent wetland (inverse relationship) was only a marginally significant predictor of consumption of all wetland-dependent prey combined (table 4) and other wetland variables were poor predictors.

DISCUSSION

Importance of Wetland Habitats and Avian Prey

Prodigious use of wetland-dependent prey species by nesting Great Horned Owls in late

Table 4.—*Most parsimonius linear regression models that best explain variance in percentage biomass contribution or daily biomass consumption rates (DBC, g/day) of major prey of Great Horned Owls (*Bubo virginianus*), northwestern North Dakota, 1986-1987.*

Prey model	DV[1]	IV[2]	Coefficient Standardized estimate (b')	P[3]	Fit of model R[2]	F	P
Vole I	DBC	No. juvenile owls	0.71	0.012	0.513	5.26	0.027
		Hayland near perches[4] (log)[5]	0.43	0.089			
Vole II	DBC	Year (vole abundance)[6]	0.51	0.015	0.689	8.86	0.002
		Number of juvenile owls	0.45	0.032			
		Percent hayland (log)	0.36	0.065			
Rails	DBC	Idle prairie near perches (log) (inverse)			0.265	6.14	0.024
Duck I	DBC	Percent pasture	0.55	0.003	0.492	9.19	0.002
		Distance to road or farmstead	0.39	0.028			
Duck II	DBC	Distance to nearest pasture (log)	-0.47	0.014	0.414	6.70	0.006
		Distance to road or farmstead	0.45	0.019			
Duck III DBC (adult ducks)		Percent pasture	0.49	0.015	0.369	5.56	0.013
		Percent aspen	0.32	0.099			
Duck IV DBC (juvenile ducks)		Percent semi-permanent wetland			0.175	4.23	0.053
Wetland prey[7]	DBC	Distance to semipermanent wetland (inverse)			0.177	4.31	0.051

[1] Dependent variable = percentage dietary biomass (%) or total daily biomass consumption rate in g/day (DBC) represented by a prey category.

[2] Independent variable(s): measures of nesting area habitat, year effect, and number of young.

[3] Probability of $\underline{t}$ in reduced model test for coefficient.

[4] Area (ha) within nesting area ≤ 100 m from perches > 6 m tall.

[5] Data were log transformed.

[6] Year effect: 1986 and 1987 vole abundance index (0.1 and 12.4 captures/100 trap-nights [Murphy 1993]).

[7] Collectively: grebes, ducks, rails, certain passeriforms and shorebirds (e.g., Yellow-headed Blackbird, Black Tern), muskrat, amphibians.

spring and early summer was a major finding of this study. Such prey were far less important to nesting Great Horned Owls in the Great Lakes States (Errington *et al.* 1940, Petersen 1979) and boreal forest ecotone (Rusch *et al.* 1972). Use of grebes, Sora, Yellow-headed and Red-winged Blackbirds, juvenile muskrat, and especially ducks and coots was so extensive in this study that wetlands clearly were major foraging sites of adult Great Horned Owls. Some regression models suggested variation in use of duck prey related directly to the extent or, inversely, proximity of pasture (grazed native prairie). Some adult and juvenile ducks could have been captured in such uplands (e.g., hens at nests, broods traveling between wetlands), but others such as coots and grebes occur almost exclusively in wetlands (Kantrud 1985, Kantrud and Stewart 1984).

Few regression models adequately predicted owl use of wetland-dependent prey. For example, there was almost no relationship between use of ducks or coots and proximity and extent of wetlands within owl nesting areas. This suggests Great Horned Owls sought wetland prey regardless of proximity or abundance of wetland habitats. Thus, if abundance of wetland-dependent prey related directly to occurrence of wetland habitats, owls did not consistently prey on what was locally most abundant, a relationship McInvaille and Keith (1974) also noted among Great Horned Owls, waterbirds, and wetlands in Alberta. Instead, my data support the assertion of Rusch *et al.* (1972) that wetlands are an exception to a direct, prey habitat-prey use relationship and that prey are more available and vulnerable to the owl in wetland sites than expected. Great Horned Owls may have used wetland-dependent prey extensively because quaking aspen comprised most elevated hunting perches on my study area and typically bordered wetlands. Prairie wetlands bordered by aspen probably are rich food patches (Krebs 1973, Pyke *et al.* 1977) for foraging Great Horned Owls due to high prey density and diversity (Kantrud and Stewart 1984, Kantrud *et al.* 1989).

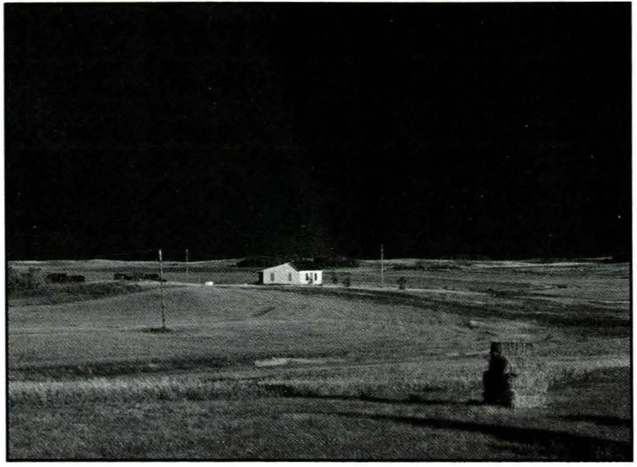
Overwhelming importance of avian prey to Great Horned Owls in my study was unusual although not unique. A cursory survey of Great Horned Owl diets in central North Dakota also suggested dominance by avian prey (Gilmer *et al.* 1983). Snyder and Wiley (1976) characterized Great Horned Owl diets in North America as 77 percent (frequency) mammalian and 6 percent avian prey, and subsequent reviews have closely corroborated this preponderance of mammalian prey (Marti and Kochert 1995). I attribute importance of birds in owl diets to relatively abundant avifauna associated with mixed grass prairie and numerous wetlands in the Missouri Coteau (Kantrud *et al.* 1989, Stewart 1975). At least 47 species of birds were prey of Great Horned Owls in this study, representing more than one-half of area breeding species (Stewart 1975). Scarcity of other, usually staple, prey especially leporids (Errington *et al.* 1940) also contributed to high use of avian prey. For example, nesting Great Horned Owls in the nearby Aspen Parkland region of Canada, where wetlands also abound, rely heavily on snowshoe hares (*Lepus americana*) and rodents (Bird 1929, Houston 1987). Decreased use of avian prey from eastern to western U.S. has been suggested (mean frequencies, 24 and 6 percent avian prey [Marti and Kochert 1995]). The northern Great Plains apparently form a gap in the knowledge of Great Horned Owl predation and trophic relationships and may supply further data that challenge generalizations about patterns in this owl's diet. Dietary diversity I recorded (overall food niche breadth, by prey class) exceeded that of most other Great Horned Owl populations studied in North America (Marti and Kochert 1995), a disparity that also can be attributed largely to the importance of avian prey in this study. Previously, Great Horned Owl trophic diversity was thought to be lowest in grassland biomes (Donazar *et al.* 1989).

The mean prey size I observed (197 g) was more than 2.5 times greater than a geometric mean reported for North American Great Horned Owls by Marti and Kochert (1995). I attribute this marked difference to the major contribution of relatively large, wetland-dependent birds (ducks, American Coot, grebes) as prey in this study, instead of small rodents typically predominant in the owl's diet elsewhere in North America. Relatively large prey from wetlands, especially ducks, may have been selected most often due to high bioenergetic profitability (Stalmaster and Gessaman 1982). Short nights (7 hours) during early summer in the far northern Great Plains may limit numbers of forays that can be made by Great Horned Owl pairs and thus preclude delivery of adequate numbers of smaller, less rich prey (e.g., mice, voles), especially for pairs tending several owlets.

Use of Upland Prey

Use of jackrabbits, deer mice, and ground squirrels indicated that Great Horned Owls did not hunt wetlands exclusively. Predation on spermophiles, especially thirteen-lined ground squirrels that are believed to be completely diurnal (Jones *et al.* 1983:144), suggested Great Horned Owl pairs hunted beyond dusk to dawn, or that the ground squirrels were crepuscular. Besides selecting relatively large prey, Great Horned Owls could compensate for a limited number of nocturnal hours in the northern Great Plains by extending their crepuscular activity. Relative low occurrence of leporid prey was expected because snowshoe hares and cottontails (*Sylvilagus* spp.) were lacking on the study area and white-tailed jackrabbits were scarce. Extent of predation on juvenile jackrabbits (N = 95 detected on platforms) despite their apparent scarcity, however, implied some selection for leporid prey. Leporids tend to be main prey of Great Horned Owls in temperate deciduous forests, whereas voles and a suite of other species of small rodents typically dominate diets in northern coniferous forests and deserts, respectively (Donazar *et al.* 1989)

Great Horned Owls also preyed heavily on meadow voles, another prey not strictly tied to wetlands. However, the vole inhabits dense, mesic vegetation (Jones *et al.* 1983:222) that typically occurs on wetland edges and within ephemeral and temporary prairie wetlands (Kantrud *et al.* 1989). Indeed, Great Horned Owl predation on meadow voles in southwestern Idaho appeared related to wetlands (Marti and Kochert 1996). But, regression models from my study suggested a link between vole use and hayland. Owls preyed on voles before hay was harvested, when it was relatively tall (to 45 cm). Although tall vegetation affords cover for small mammal prey of some raptors (Bechard 1982), Great Horned Owls can forage in vegetation up to 45-60 cm tall (Frounfelker 1977), especially when elevated perches occur nearby (Petersen 1979). A regression model in this study suggested a direct link between vole use and amount of hayland near hunting perches.



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Cropland, mostly wheat, and grass-alfalfa hayland comprised 31 and 5 percent of the study area, respectively. About one-third of croplands were fallowed. Hay was harvested during July.

Rare predation on Sharp-tailed Grouse was a startling result because the species was common and conspicuous. For example, I noted four leks each with 18-30 displaying male grouse, on about 25 km^2 of Lucy Township. These were within Great Horned Owl nesting areas I monitored beginning in May when grouse were active on leks at dawn and dusk. Rusch *et al.* (1972) suggested male Sharp-tailed Grouse in Alberta were vulnerable to Great Horned Owl predation in spring, but Houston (1960) found little evidence of owl predation on Sharp-tailed Grouse in Saskatchewan and Berger *et al.* (1963) noted raptors seldom preyed on cogeneric Greater Prairie Chickens (*T. cupido*) on leks in Wisconsin. Perhaps owls rarely preyed on grouse because wetlands were attractive foraging sites.

SUMMARY AND CONCLUSIONS

Great Horned Owls nesting on mixed farm- and rangelands in the Missouri Coteau of northwestern North Dakota relied heavily on avian prey associated with prairie wetlands during late spring through early summer. High diet diversity and mean prey weight relative to reports from previous studies of the owl's diet were attributed to this predominance of avian, wetland-dependent prey. Adult and juvenile ducks, American Coots, passerines especially juvenile blackbirds, and meadow voles and deer mice were most important prey overall. Dietary composition varied among owl pairs, but the variation was not always clearly related to habitat or land use because wetlands probably were selected as foraging sites regardless of prevalence or distance from nests. Availability of adjacent perches likely was an important determinant of opportunistic use of wetlands by owls, although this was not consistently suggested among regression models. Differences in prey preference among owl pairs also may have clouded prediction of owl diet based on wetland habitat within nesting areas. Reliance on avian prey, especially that from wetlands, may not be as strongly evident in other physiographic subregions of the northern Great Plains, which have lower wetland abundance than the Missouri Coteau and far fewer wetlands with adjacent perches than on the Coteau in northwestern North Dakota. Also, wetland-dependent prey may be more or less available during years of abundant moisture or drought, than they were in near average wetland conditions during this study. I suspect vulnerability of such prey to Great Horned Owl predation is elevated by rapid drying of seasonal and some semipermanent wetlands that often occurs as summer progresses (Kantrud *et al.* 1989). Regardless, results of this study contest assertions that the owl is essentially a mammal predator across its range in North America (Marti and Kochert 1995, 1996; Snyder and Wiley 1976) and suggest exceptions to current thought on the species' trophic relationships may occur in the relatively understudied Great Plains, at least where prairie wetlands are an important landscape feature.

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LITERATURE CITED

Bechard, M.J. 1982. Effect of vegetative cover on foraging site selection by Swainson's hawk. Condor. 84: 153-159.

Bent, A.C. 1938. Life histories of North American birds of prey, part 2. U.S. Natl. Mus. Bull. 170. Washington, DC: Smithsonian Institute. 465 p.

Berger, D.D.; Hamerstrom, F.; Hamerstrom, F.N., Jr. 1963. The effect of raptors on Prairie Chickens on booming grounds. Journal of Wildlife Management. 27: 778-791.

Bird, R.D. 1929. The Great Horned Owl in Manitoba. Canadian Field-Naturalist. 43: 79-83.

Bluemle, J.P. 1977. The face of North Dakota: the geologic story. North Dakota Geological Survey Education Series No. 11. 73 p.

Collopy, M.W. 1983. A comparison of direct observations and collections of prey remains in determining the diet of Golden Eagles. Journal of Wildlife Management. 47: 360-368.

Craighead, J.J.; Craighead, F.C. 1956. Hawks, owls and wildlife. Harrisburg, PA: Stackpole Co. 443 p.

Dixon, W.J. 1983. BMDP statistical software. Berkeley, CA: University of California Press. 733 p.

Donazar, J.A.; Hiraldo, F.; Delibes, M.; Estrella, R.R. 1989. Comparative food habits of the Eagle Owl *Bubo bubo* and the Great Horned Owl *Bubo virginianus* in six Palearctic and Nearctic biomes. Ornis Scandinavica. 20: 298- 306.

Dunning, J.B. 1984. Body weights of 686 species of North American birds. Western Bird Banding Association, Monograph No. 1. 38 p.

Errington, P.L.; Hamerstrom, F.; Hamerstrom, F.N., Jr. 1940. The Great Horned Owl and its prey in north-central United States. Iowa Agricultural Experiment Station Research Bulletin. 227: 758-850.

Frounfelker, C.R. 1977. Prey selection of the Great Horned Owl with reference to habitat and prey availability. Moscow, ID: University of Idaho. 62 p. M.S. thesis.

Gilmer, D.S.; Konrad, P.M.; Stewart, R.E. 1983. Nesting ecology of Red-tailed Hawks and Great Horned Owls in central North Dakota and their interactions with other large raptors. Prairie Naturalist. 15: 133-143.

Houston, C.S. 1960. 1960 - the year of the owls. Blue Jay. 18: 105-110.

Houston, C.S. 1987. Nearly synchronous cycles of the Great Horned Owl and snowshoe hare in Saskatchewan. In: Nero, R.W.; Clark, R.J.; Knapton, R.J.; Hamre, R.H., eds. Biology and conservation of northern forest owls; Symposium proceedings; 1987 February 3-7; Winnipeg, MB. Gen. Tech. Rep. RM-142. Fort Collins, CO: U.S. Deaprtment of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 56-58.

James, T.R.; Seabloom, R.W. 1969. Aspects of growth in the white-tailed jackrabbit. Proceedings of the North Dakota Academy of Science. 23: 7-14.

Jones, J.K., Jr.; Armstrong, D.M.; Hoffman, R.S.; Jones, C. 1983. Mammals of the Northern Great Plains. Lincoln, NE: University of Nebraska Press. 379 p.

Kantrud, H.A. 1985. American Coot habitat in North Dakota. Prairie Naturalist. 17: 23-32.

Kantrud, H.A.; Stewart, R.E. 1984. Ecological distribution and crude density of breeding birds on prairie wetlands. Journal of Wildlife Management. 48: 426-437.

Kantrud, H.A.; Krapu, G.L.; Swanson, G.A. 1989. Prairie basin wetlands of the Dakotas: a community profile. U.S. Fish and Wildlife Service, Biological Report No. 85(7.28). 111 p.

Korschgen, L.J.; Stuart, H.B. 1972. Twenty years of avian predator-small mammal relationships in Missouri. Journal of Wildlife Management. 36: 269-282.

Krebs, J.R. 1973. Behavioral aspects of predation. In: Perspectives in ethology. New York, NY: Plenum Press: 73-111.

Marti, C.D. 1987. Raptor food habits studies. National Wildlife Federation, Scientific and Technical Series. 10: 67-80.

Marti, C.D.; Kochert, M.N. 1995. Are Red-tailed Hawks and Great Horned Owls diurnal-nocturnal dietary counterparts? Wilson Bulletin. 107: 615-628.

Marti, C.D.; Kochert, M.N. 1996. Diet and trophic characteristics of Great Horned Owls in southwestern Idaho. Journal of Field Ornithology. 67: 499-506.

McInvaille, W.B., Jr.; Keith, L.B. 1974. Predator-prey relations and breeding biology of the Great Horned Owl and Red-tailed Hawk in central Alberta. Canadian Field-Naturalist. 88: 1-20.

Murphy, R.K. 1993. History, nesting biology, and predation ecology of raptors in the Missouri Coteau of northwestern North Dakota. Bozeman, MT: Montana State University. 212 p. Ph.D. dissertation.

Neter, J.; Wasserman, W.; Kutner, M.H. 1985. Applied linear statistical models. Homewood, IL: Irwin, Inc. 1,127 p.

Orians, G.; Kuhlman, F. 1956. Red-tailed Hawk and Horned Owl populations in Wisconsin. Condor. 58: 371-385.

Petersen, L. 1979. Ecology of Great Horned Owls and Red-tailed Hawks in southeastern Wisconsin. Tech. Bull. 111. Wisconsin Department of Natural Resources. 63 p.

Petersen, L.R.; Keir, J.R. 1976. Tether platforms - an improved technique for raptor food habits study. Journal of Raptor Research. 10: 21-28.

Pyke, G.H.; Pulliam, H.R.; Charnov, E.L. 1977. Optimal foraging: a selective review of theory and tests. Quarterly Review of Biology. 52: 137-154.

Rusch, D.H.; Meslow, E.C.; Doerr, P.D.; Keith, L.B. 1972. Response of Great Horned Owl populations to changing prey densities. Journal of Wildlife Management. 36: 282-296.

Sargeant, A.B.; Greenwood, R.J.; Sovada, M.A.; Shaffer, T.L. 1993. Distribution and abundance of predators that affect duck production - Prairie Pothole Region. Resour. Publ. 194. U.S. Fish and Wildlife Service. 96 p.

SAS Institute. 1989. SAS/STAT user's guide, version 6, 4th ed. Cary, NC: SAS Institute, Inc. 846 p.

Snyder, N.F.R.; Wiley, J.W. 1976. Sexual size dimorphism in hawks and owls of North America. American Ornithologists' Union, Ornithological Monograph. 20. 96 p.

Sokal, R.R.; Rohlf, F.J. 1981. Biometry. New York, NY: W.H. Freeman Co. 859 p.

Stalmaster, M.V.; Gessaman, J.A. 1982. Food consumption and energy requirements of captive Bald Eagles. Journal of Wildlife Management. 46: 646-654.

Stewart, R.E. 1975. Breeding birds of North Dakota. Fargo, ND: Tri-college Center for Environmental Studies. 295 p.

Stewart, R.E.; Kantrud, H.A. 1971. Classification of natural ponds and lakes in the glaciated prairie region. Resour. Publ. 92. U.S. Fish and Wildlife Service. 57 p.

Voous, K.H. 1988. Owls of the Northern Hemisphere. Cambridge, MA: MIT Press. 320 p.

Appendix A.—*Prey recorded at 22 Great Horned Owl (*Bubo virginianus*) nesting areas in the Missouri Coteau of northwestern North Dakota, 1986-1987.*

Mammals
Leporids
White-tailed jackrabbit (*Lepus townsendii*)

Ground squirrels
Richardson's g. squirrel (*Spermophilus richardsonii*)
Thirteen-lined ground squirrel (*S. tridecemlineatus*)
Franklin's ground squirrel (*S. franklinii*)[1]

Mice
Deer mouse (*Peromyscus maniculatus*)
Western or meadow jumping mouse (*Zapus* spp.)
Olive-backed pocket mouse (*Perognathus fasciatus*)[1]
N. grasshopper mouse (*Onychomys leucogaster*)[1]
House mouse (*Mus musculus*)[1]

Voles
Meadow vole (*Microtus pennsylvanicus*)
S. red-backed vole (*Clethrionomys gapperi*)[1]

Other Rodents
Muskrat (*Ondatra zibethicus*)
Norway rat (*Rattus norvegicus*)

Miscellaneous mammals
Short-tailed shrew (*Blarina brevicauda*)
Masked shrew (*Sorex cinereus*)
Least weasel (*Mustela nivalis*)[1]
Striped skunk (*Mephitis mephitis*)[2]

Birds
Grebes
Horned grebe (*Podiceps auritus*)
Eared grebe (*P. nigricollis*)
Pied-billed grebe (*Podilymbus podiceps*)

Ducks
Green-winged teal (*Anas carolinensis*)
Mallard (*A. platyrhynchos*)
N. pintail (*A. acuta*)
Blue-winged teal (*A. discors*)
N. shoveler (*A. clypeata*)
Gadwall (*A. streptera*)
American wigeon (*A. americana*)
Redhead (*Aythya americana*)
Lesser scaup (*A. affinis*)
Ruddy (*Oxyura jamaicensis*)

Grouse and Partridge
Sharp-tailed grouse (*Tympanuchus phasianellus*)
Gray partridge (*Perdix perdix*)

Rails
American coot (*Fulica americana*)
Sora (*Porzana carolina*)
Virginia rail (*Rallus limicola*)[1]

Shorebirds
Killdeer (*Charadrius vociferus*)
American avocet (*Recurvirostera americana*)[1]
Upland sandpiper (*Bartramia longicauda*)
Willet (*Catoptrophorus semipalmatus*)[1]
Common snipe (*Gallinago gallinago*)[1]
Wilson's phalarope (*Phalaropus tricolor*)
Black tern (*Chlidonias niger*)

Passeriforms
E. kingbird (*Tyrannus tyrannus*)
Horned lark (*Eremophila alpestris*)
American crow (*Corvus brachyrhynchos*)
House wren (*Troglodytes aedon*)
Brown thrasher (*Toxostroma rufum*)
Unknown warblers (Parulinae)
Unknown sparrows (Emberizinae)
Bobolink (*Dolichonyx oryzivorus*)
Red-winged blackbird (*Aeglaius phoeniceus*)
Western meadowlark (*Sturnella neglecta*)
Yellow-headed blackbird (*Xanthocephalus xanthocephalus*)
Brewer's blackbird (*Euphagus cyanocephalus*)
Common grackle (*Quiscalus quiscula*)
Brown-headed cowbird (*Molothrus ater*)
Baltimore oriole (*Icterus galbula*)
Unknown blackbirds (Icterinae)

Domestic chicken

Miscellaneous
American bittern (*Botaurus lentiginosus*)[2]
Black-crowned night heron (*Nycticorax nycticorax*)[2]
Canada goose (*Branta canadensis*)[2,3]
Mourning dove (*Zenaida macroura*)[1]
N. saw-whet owl (*Aegolius acadicus*)[2,4]
N. harrier (*Circus cyaneus*)[2]
Yellow-shafted flicker (*Colaptes auratus*)[1]

Amphibians
Tiger salamander (*Ambystoma tigrinum*)
N. leopard frog (*Rana pipiens*)[2]

Reptiles
Plains garter snake (*Thamnophis radix*)[2]

Insects
Grasshoppers, crickets (Orthoptera: Oedipodinae)
Giant water bug (Hemiptera: Belostomatidae)[1]

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[1] Less than five individuals recorded.
[2] One individual recorded.
[3] Juvenile.
[4] Probably a spring migrant instead of a local breeding species (Stewart 1975:161).

Mortality Causes in British Barn Owls (*Tyto alba*), Based on 1,101 Carcasses Examined During 1963-1996

I. Newton, I. Wyllie, and L. Dale[1]

Abstract.—During 1963-1996, 1,101 Barn Owl (*Tyto alba*) carcasses were received for autopsy and chemical analysis. Much larger numbers were received per month outside the breeding season than within it. A peak in the monthly mortality of first year birds occurred in autumn (November) and a peak in the mortality of adults in late winter (March).

The main causes of recorded deaths were collisions (mostly with road traffic) and starvation. No great seasonal variation occurred in the main causes of recorded deaths. Among accident victims, the mean weight of females (305 g) was about 5 percent greater than that of males (291 g). Most starved birds of both sexes weighed less than 240 g.

Organochlorine pesticide victims formed 20 percent of all dead Barn Owls obtained during 1963-1970, and a decreasing proportion thereafter. None was recorded after 1976 when the use of aldrin/dieldrin was greatly curtailed. During the 1980s and 1990s, increasing proportions of birds contained residues of second generation rodenticides, but relatively few at sufficient level to have caused their death.

Although the numbers of Barn Owls (*Tyto alba*) breeding in Britain and some other parts of western Europe have declined during the present century, there is no consensus view of the underlying causes. Changes in agriculture, notably the reduction in area of rough grassland and its associated *Microtus* voles, have probably greatly reduced the food-supply of the species. At the same time, in some regions, the loss of old trees and farm buildings that provided nest sites might have reduced Barn Owl numbers below the level that the contemporary food-supply would permit, as might the increased mortality imposed by road traffic and pesticides (Bunn *et al.* 1982, de Bruijn 1994, Shawyer 1987, Taylor 1994). In this paper, we present information on the causes of death of 1,101 Barn Owls found dead in Britain during 1963-1996, and sent to Monks Wood Research Station for study. We focus on organochlorine pesticides, notably aldrin and dieldrin, as a major cause of Barn Owl deaths during the 1960s and 1970s, and on new rodenticides as increasing contaminants during the 1980s and 1990s. The rodenticides concerned include difenacoum, bromadiolone, brodifacoum, and flocoumafen, all of which are marketed under several different trade names.

Findings on carcasses analyzed to 1989 were summarized by Newton *et al.* (1991). Since that date the number of Barn Owl carcasses received has increased from 627 to 1,101, and some causes of death have changed in importance. Other studies of mortality in British Barn Owls have been reported by Shawyer (1987), based on 629 specimens found during 1982-1986, and by Glue (1971), based on 320 ring recoveries, covering the period 1909-1970.

PROCEDURE

Carcasses were obtained from most parts of Britain, in response to regular advertisements placed in ornithological magazines and journals. All carcasses were requested, regardless of the cause of death. On receipt, each carcass was weighed, marked and then stored at -20°C until it could be examined, up to several months later. Age classes (juvenile or adult) were diagnosed from 1988 onwards, mainly on plumage. Juveniles (in their first year) had unabraded primaries of uniform bloom, more pointed than those of adults, and outermost primary feathers (number 11, small and hidden) that were pure white, not grey. Some also had fault bars running in the same position across all tail feathers. On dissection, juvenile females before the breeding season had a thin straight oviduct, rather than the thicker convoluted oviduct of a bird that had laid. Birds of all ages were sexed by their gonads, but most males had fewer dark spots on the underside than females. Not all specimens could be aged or sexed, however, because some had been previously skinned or were badly damaged. Full information was therefore not obtained from every bird, which is one reason why the totals given in the different tables and figures of this paper vary.

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For autopsy, the unfrozen carcass was opened up and examined for any obvious parasites, lesions or other abnormalities. The findings were used, along with information from the sender, to diagnose the cause of death. Typically, collision victims had extensive bruising and broken bones, and many were found at roadsides indicating that they were traffic victims. Starved birds were low in weight, with wasted breast muscles, no body fat, and empty blackened or greenish intestines. Diseased birds showed obvious lesions, particularly in liver, kidneys or lungs, or contained parasites; and many were also thin. Shot birds contained lead pellets or pellet wounds. Diagnosis of other mortality causes, such as drowning and electrocution, was dependent primarily on information from the sender, together with the lack of any conflicting evidence from autopsy. Identification of pesticide or rodenticide victims was dependent mainly on chemical analysis, together with the lack of any other obvious mortality cause. Some organochlorine victims that were found still alive were reported to die in spasms. For certain birds (8.4 percent of the total), in the absence of any evidence, the cause of death was classed as 'unknown'.

Many of the birds examined showed signs of hemorrhaging, which differed according to cause of death. Accident victims typically bled heavily around the site of impact, while some organochlorine victims showed hemorrhaging of certain internal organs, including brain, lungs, heart, and foregut (Newton *et al.* 1982). Other work revealed that rodenticide victims typically showed faint subcutaneous bleeding along the keel and on the skull, and external bleeding around the leg joints and beak (Newton *et al.* 1990). However, some organochlorine and rodenticide victims showed no obvious bleeding. Hemorrhaging was therefore not used as the sole diagnosis of any mortality cause, only along with other evidence, including chemical analysis.

After autopsy, a piece of liver was removed and analyzed for organochlorine residues of DDE (from the insecticide DDT), HEOD (from the insecticides aldrin and dieldrin), HE (from the insecticide heptachlor) and PCBs (polychlorinated biphenyls from various industrial products) (for methods of analysis, see Newton *et al.* 1990). Organochlorine analyses almost ceased after 1977, partly on grounds of cost, when residues fell to small levels after the last major restriction in 1976 in aldrin-dieldrin use. Only a random sample of 50 livers was analyzed for organochlorines after 1977. Although residues were detected in all these livers, the levels were low, invariably less than one tenth of the levels normally associated with death.

After considering the available data, Cooke *et al.* (1981) concluded for various birds of prey that a concentration in liver of 10 ppm or more HEOD (in wet weight) or 100 ppm or more DDE could be taken as indicative of organochlorine poisoning. Little information is available for heptachlor, but De Witt *et al.* (1960) found 6-20 ppm HE in tissues of various birds poisoned by this chemical. Organochlorine victims often showed other symptoms, however, such as internal hemorrhaging (Newton *et al.* 1982) and usually died with muscle tremors or convulsions.

Specific information on the HEOD levels in livers of owls that had died of dieldrin poisoning was obtained at the London Zoo, where in a 30-month period 55 owls of 21 species died (Jones *et al.* 1978). Their deaths were traced to high dieldrin levels in the mice that they were fed, the mice having been kept on sawdust bedding derived from dieldrin-treated timber. Of 22 obvious dieldrin casualties that were analyzed, HEOD levels in liver ranged between 13 and 46 ppm, with a geometric mean of 29 ppm.

Since 1983, liver samples were analyzed for residues of 'second generation' anticoagulant rodenticides, namely bromadiolone, difenacoum, brodifacoum, and flocoumafen, which have been implicated in Barn Owl mortality (Newton *et al.* 1990, Shawyer 1987). Little information is available on liver residue levels associated with death in Barn Owls, but some figures are given later in this paper, to be added to the figures of 0.5-1.3 ppm given for brodifacoum by Newton *et al.* (1990), 0.3-1.7 ppm given by Wyllie (1996) for bromodialone, and 0.9 ppm for flocoumafen given by Newton *et al.* (1994).

RESULTS

Annual Cycle

Although Barn Owls in Britain can be found breeding in all months from February to November, depending on vole abundance, most breeding activity occurs in April-August (Bunn *et al.* 1982, Hardy *et al.* 1982, Shawyer 1987, Taylor 1989).

Many more carcasses were received outside the breeding season than within it (fig. 1). Monthly numbers rose from August to November and remained at high level until March, declining thereafter to a low in May-July. Birds were aged (as juvenile to 31 July the next year and as adult thereafter) on a systematic basis only from 1988. From then on, in nine complete years juveniles formed 76 percent of 541 birds received (table 1). As an estimate of first-year mortality this is 14 percent higher than the 62 percent calculated by Glue (1971) from 320 ring recoveries from a longer run of years.

In our sample, juveniles predominated in the August-November period but declined in proportion thereafter, so that the two age groups had partly different periods of mortality. The number of juveniles received each month reached a peak in the autumn (November) whereas the number of adults reached a peak in late winter (March). Of 968 owls in which the sex was recorded, 495 (51 percent) were males and 473 (49 percent) were females, a ratio not significantly different from unity. There was no evidence for a change in the sex ratio of casualties through the year (table 1), except that more males than females were received in the breeding season. This could be attributed to the sex difference in breeding roles (the male does the hunting while the female tends the eggs and young).

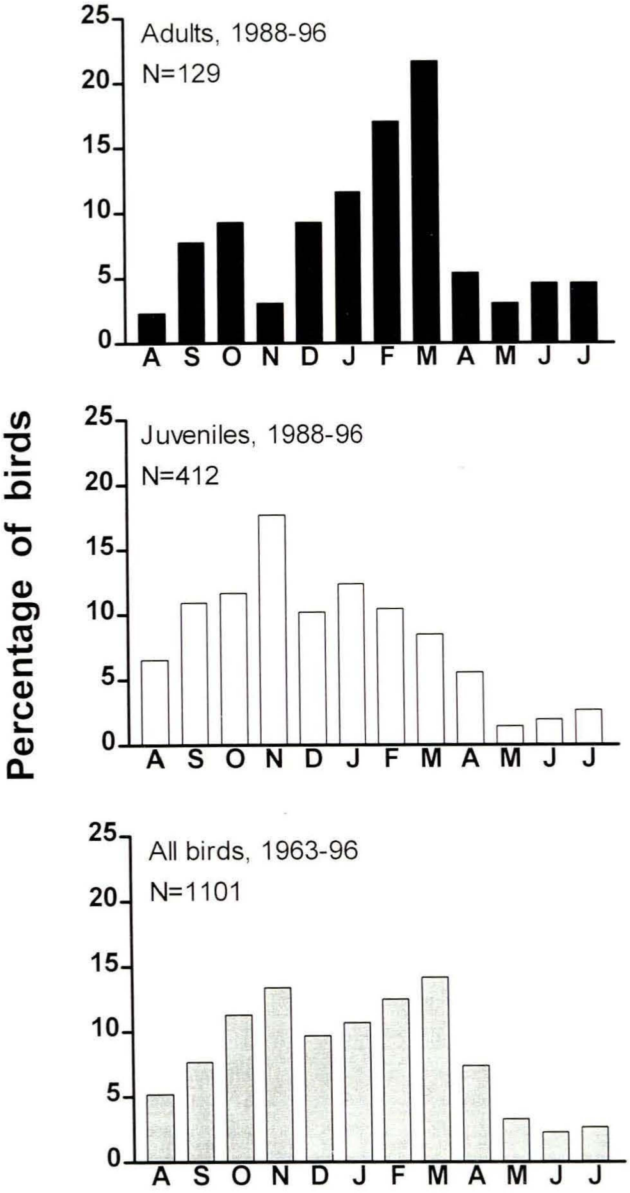

Figure 1.—*Percentage of Barn Owl (*Tyto alba*) carcasses found in Britain in different months. The lower diagram includes all birds received over the 34 year study period, and the others refer separately to first-year birds and adults respectively, which were distinguished from 1988.*

Because some important prey species (notably *Microtus agrestis*) of the Barn Owl fluctuate in roughly 3-4 year cycles of abundance, one might have expected some cyclic variation in the number of owl carcasses received at Monks Wood. This was not apparent on a national scale, however, and too few carcasses were obtained from particular regions to check for more local cycles in mortality.

Table 1.—*Sex and age ratios among Barn Owls (*Tyto alba*) in Britain found dead in different months.*

	1963-1996		1988-1996	
	Male	**Female**	**Juvenile**	**Adult**
January	55	48	51	15
February	59	64	43	22
March	70	70	35	28
April	32	32	23	7
May	20	10	6	4
June	13	10	8	6
July	14	9	11	6
August	34	19	27	3
September	37	38	45	10
October	47	62	48	12
November	55	70	73	4
December	59	41	42	12
Total	495	473	412	129
Percent	51%	49%	76%	24%

Mortality Causes

Over the year as a whole, 54 percent of all recorded deaths were attributable to some form of collision or other accident (table 2). Within this category the most prevalent were road traffic victims, which formed at least 45 percent of all deaths. Minor causes included other forms of trauma, drowning in water-troughs, and electrocution.

'Natural' causes accounted for 31 percent of all recorded deaths. The most important was starvation (26 percent of all deaths), followed by disease/parasitism (3 percent), and then predation (2 percent). Most of the diseased birds were also thin, so it was often uncertain whether food-shortage or infection was the primary cause of death. Several birds classed as diseased had extensive lesions on the kidneys, liver or heart, others had infected lungs, while in one the digestive tract was heavily infested with nematode worms. The only predators identified with certainty were domestic cat and dog.

The remaining birds had been shot (1 percent) or were diagnosed as victims of organochlorine pesticide (mostly dieldrin) poisoning (5 percent), or rodenticide poisoning (1 percent). All the birds tested for organochlorines had residues in their livers but mostly at levels considered to be sublethal. Of 51 birds diagnosed as aldrin/dieldrin victims, 10 had HEOD levels of 6-10 ppm in liver, 29 had levels of 10-20 ppm, 8 had levels of 21-30 ppm, 3 had levels of 31-40 ppm, and 1 had 44 ppm (Newton *et al.* 1991). All these birds (including those with less than 10 ppm HEOD in liver) had other symptoms of organochlorine poisoning (most often convulsions prior to death), and no other obvious cause of mortality. In addition, two road traffic victims had 11 and 14 ppm HEOD, in their livers, so in the absence of the collision, they might have died anyway from poisoning.

Table 2.—*Recorded causes of deaths in Barn Owls (*Tyto alba*) found dead in Britain during 1963-1996.*

	Number	**Percent**
Natural causes	328	30.7
Starvation	275	25.8
Disease	35	3.3
Predation	18	1.7
Accidents	573	53.7
Road casualties	477	44.7
Other trauma	80	7.5
Drowned	12	1.1
Electrocuted	4	0.4
Other human-related causes	76	7.1
Poisoned	65	6.1
Shot	11	1.0
Unknown causes	90	8.4

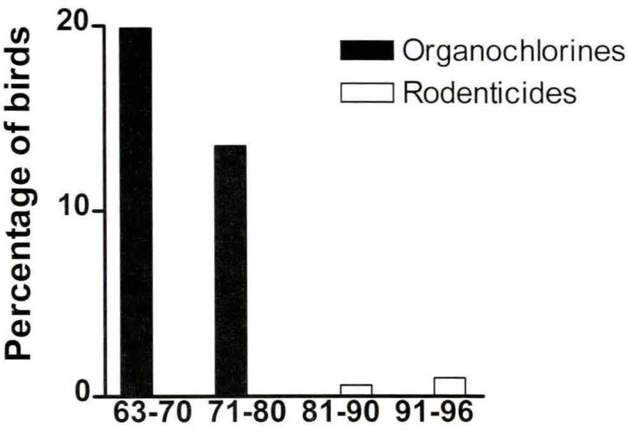

Figure 2.—*Proportion of Barn Owls (*Tyto alba*) examined in Britain whose deaths were attributed to organochlorine or rodenticide poisoning in four successive periods.*

Table 3.—*Percentage of Barn Owls (*Tyto alba*) from Britain that contained rodenticides in different periods.*

	Number of owls analyzed	Number (percent) containing residues
1983-1984	18	1 (6)
1985-1986	75	9(12)
1987-1988	61	8(13)
1989-1990	133	31(23)
1991-1992	139	41(29)
1993-1994	131	42(32)

Significance of variation between periods: $x^2_5 = 20.4$, $P < 0.001$.

The geometric mean HEOD level in all these birds was 14.3 ppm. Two other deaths were attributed to poisoning by heptachlor epoxide, and were associated with liver levels of 14.4 and 26.0 ppm HE, and two to poisoning by DDE (130 ppm and 270 ppm). The latter also contained 55 ppm of TDE, another breakdown product of DDT. In addition, one of the birds classed as a HEOD victim also contained 700 ppm DDE. Some of these apparent pesticide victims were thin, so that loss of body fat may have contributed to high residue levels in the liver (Newton *et al.* 1991).

Of 557 birds examined during 1983-1994, 132 (24 percent) were found to contain residues of rodenticides, either difenacoum, brodifacoum, bromadiolone, flocoumafen or more than one of these compounds (table 3). Moreover, the proportion of birds in which residues were detected increased over the years, reaching around 32 percent in 1993-1994. This reflected the increasing use of these chemicals as warfarin replacements and showed that Barn Owls have become increasingly exposed to them.

In total, however, only eight birds were diagnosed as having died of rodenticide poisoning. In the seven that showed typical hemorrhage symptoms, the following residues (mg kg^{-1}) were detected in livers: (1) 0.13 bromadiolone, (2) 0.05 bromadiolone plus 0.003 flocoumafen plus 0.002 brodifacoum, (3) 0.17 difenacoum, (4) 1.07 bromadiolone, (5) 0.87 brodifacoum, (6) 1.72 bromadiolone plus 0.07 brodifacoum, (7) 0.33 bromadiolone. The eighth bird, that showed no hemorrhage symptoms, contained 0.42 mg kg^{-1} brodifacoum. It was classed as a rodenticide victim because of the relatively high brodifacoum level present and because it showed no other obvious cause of death.

Surprisingly, there was little seasonal variation in the prevalence of different forms of mortality, apart from the HEOD victims which came mainly in spring. Road and other accidents were the main form of loss throughout the year, and starved birds were found in every month, even in May-July. Although the birds examined might have lost weight through water loss by the time they reached us, the recorded weights should be comparable between different categories. Restricting analysis to the period October-March, outside the main breeding season, when weights of live birds are relatively stable (Taylor 1989), accident victims were the heaviest, while not unexpectedly those diagnosed on appearance as starved were the lightest (fig. 3). Among accident victims, males averaged 291 g and females averaged 5 percent heavier at 305 g. Most birds of both sexes that were classed on autopsy as starved weighed less than 240 g, and the average weights of starved birds of each sex was about 30 percent less than accident victims. Birds diagnosed as aldrin-dieldrin casualties were generally intermediate in weight between accident birds and starved birds (Newton *et al.* 1991), possibly because they had become immobilized sometime before their death. There was no obvious sex bias in any form of mortality, including drowning, which in Shawyer's (1987) sample was confined to females.

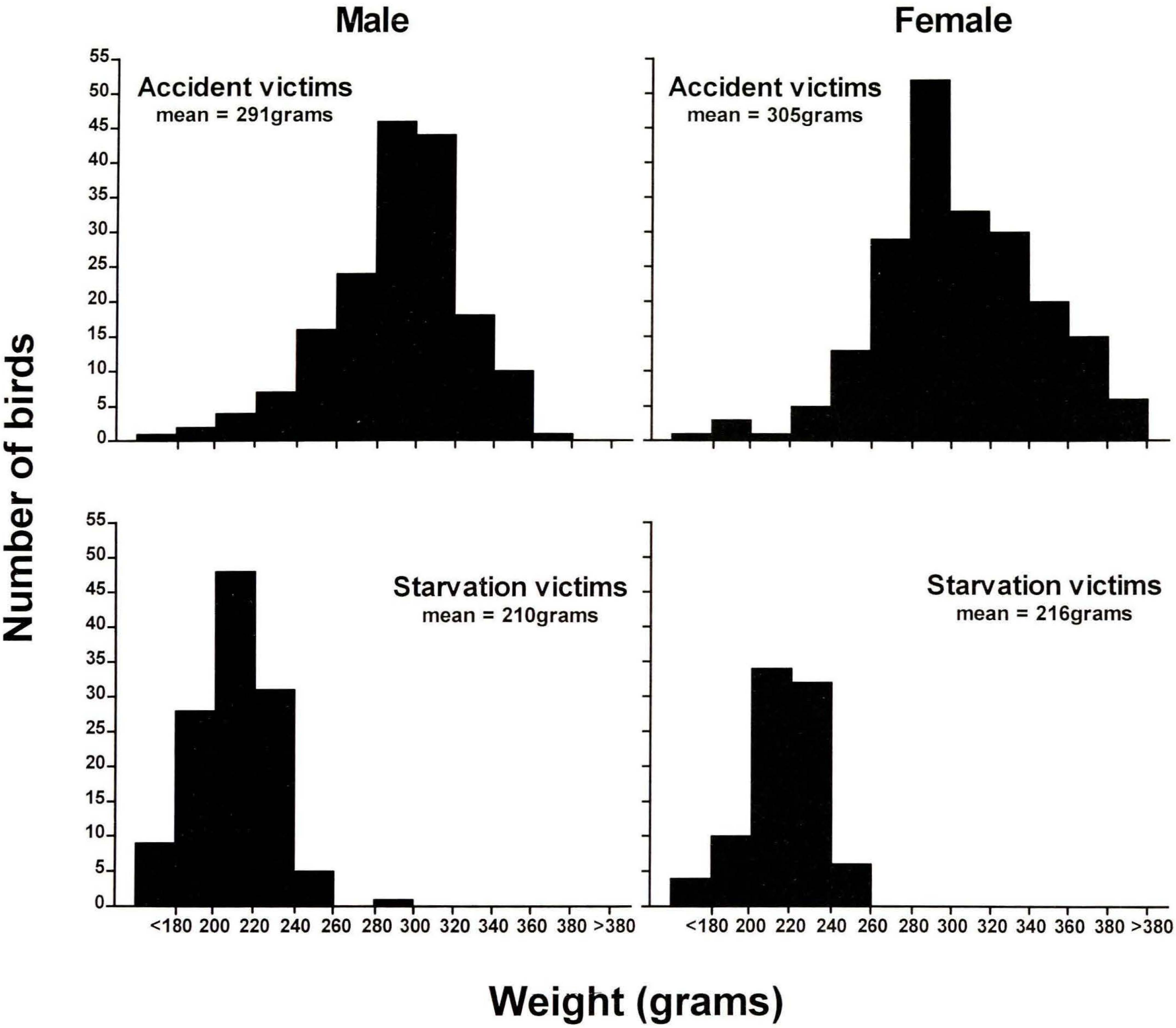

Figure 3.—*Body weight during October-March of Barn Owls (*Tyto alba*) in Britain whose deaths were attributed by autopsy to accident (trauma) or starvation.*

Some causes of death changed progressively in frequency over the years. Road casualties formed only 35 percent of the sample in 1963-1970 but had increased to 50 percent in 1991-1996. Organochlorine pesticide casualties declined from 20 percent in 1963-1970 to 14 percent in 1971-1980 and to nil in 1978-1996, although only 50 randomly-related birds were analyzed after 1977. Other causes of mortality changed in proportion, but with no consistent trends.

Frequency of Rodenticide Contamination

The dates from which various second generation rodenticides were used in Britain are given in table 4, along with their toxicities to rats and mice, compared with warfarin. In terms of LD_{50} values (lethal dose for 50 percent of a sample, expressed as mg kg^{-1} body weight), the new chemicals are roughly 100-1,000 times more toxic than warfarin. It is the combination of greater toxicity and greater persistence which gives the potential for secondary poisoning of rodent predators.

Table 4.—*Toxicities of some rodenticides.*

	Year of introduction to Britain	Lethal dose (mg kg^{-1})	
		Rat	Mouse
Warfarin	1952	185	375
Difenacoum	1975	1.80	0.80
Bromadiolone	1980	0.55	0.99
Brodifacoum	1982	0.26	0.40
Flocoumafen	1986	0.25	1.13

Their increased frequency in Barn Owl livers over the period 1983-1994 follows from their increased usage, as they have gradually replaced warfarin and other 'first generation' rodenticides. Moreover, the different chemicals have appeared in Barn Owls in proportion to their usage (table 5). It seems that our monitoring of residues has given a good reflection of changes in usage, and hence in exposure, of the British Barn Owl population.

DISCUSSION

The carcasses received probably did not represent a random cross-section of Barn Owl deaths but were biased towards those forms of mortality most readily detected by people. Ringing recoveries, which are often used in mortality studies, are biased in the same way, but our records had the additional information provided by autopsy and chemical analysis, thus revealing the significance of certain pesticides. They also revealed changes in the relative importance of different types of mortality over the years.

In important respects, our findings agree with those of Glue (1971), Shawyer (1987) and Hardy *et al.* (1982), also based on carcasses found by people. Similarities include (1) the marked seasonal pattern in recorded deaths, with peaks in autumn (due mainly to juveniles) and in late winter (due to both adults and juveniles), (2) the importance of collisions, especially with road traffic, as the major cause of reported deaths, followed by starvation, and (3) the lack of seasonal variation in the relative importance of the main causes of reported deaths.

Over the years, the proportion of recorded deaths attributed to road traffic increased: from 6 percent in 1910-1954 and 15 percent in 1955-1969 (Glue 1971, based on band recoveries), to 35 percent in 1963-1970 and 50 percent in 1991-1996 (our data). This is most readily attributed to the increasing numbers of roads, and the increasing number and speed of road vehicles over the period concerned. Associated declines in the incidence of other forms of reported mortality are notable for organochlorine poisoning, which fell from 20 percent in 1963-1976 to nil in 1981-1996, and for shooting, which fell from 12 percent in 1910-1954 to 5 percent in 1955-1969 (Glue 1971), to 1 percent in 1963-1996 (our study). The fact that few owls (n=5 in our study) were reported from railways is presumably because the tracks carry less traffic than roads and are less frequented by people able to pick up carcasses.

Accident victims were presumably over-represented in all these studies, because of ease of finding, while deaths from natural causes (especially predation) were under-represented. Some of our owls which died

Table 5.—*Rodenticide use and Barn Owl (*Tyto alba*) contamination in Britain.*

	Arable farms[1]	Livestock farms[1]	Barn Owls[2]
Number examined	565	459	449
Number with rodenticide	431	404	120
Difenacoum	62%	54%	63%
Bromadiolone	32%	37%	40%
Brodifacoum	5%	7%	14%
Flocoumafen	0.5%	1.5%	5%

[1] Based on a questionnaire survey of randomly selected farms, 1988-1989 (Olney 1991a, 1991b).

[2] Based on Barn Owls examined in 1988-1994.

from accidents were of normal weight and good condition. But others were thin, and at least 4 percent of male and 7 percent of female trauma victims weighed as little as starved birds. Poor condition may pre-dispose Barn Owls to accidents if it (a) leads them to spend more total time hunting, (b) leads them to spend relatively more time hunting in places where accidents are likely, such as road verges, or (c) makes them less able to avoid collisions. For such birds accidents are the secondary, rather than the primary, cause of death. The distinction is important because it implies that accidents have less effect on the population than their reported frequency would suggest. None-theless, most accident victims were of normal weight, so would presumably have lived considerably longer without the accident.

The seasonal pattern of reported mortality was more or less as expected from seasonal changes in population and food-supply (Taylor 1989). The May-July trough in recorded deaths coincides with the main period of breeding, when food is readily available and females are largely confined to their nests. The rise in mortality, from August to November, occurs when the Barn Owl population reaches its annual peak, through breeding. Such mortality falls mainly on the juveniles in the period when they become independent and disperse. As the breeding season extends in some years into November, the transition-dispersal period for the young is also spread over several months. Reported mortality remains high throughout the winter, but adults form a much greater proportion of casualties in February-March. By then the owl population is lower but the food-supply is also approaching its annual trough, perhaps deepened in some years by snow cover, and evidently leading to more frequent starvation and collisions.

Chemical analyses confirm that aldrin-dieldrin poisoning accounted for a large proportion of recorded Barn Owl deaths in the 1960s and 1970s. The owls examined contained some of the highest aldrin-dieldrin and heptachlor levels found in any birds of prey in Britain, including some on a par with the highest levels found in Sparrowhawks (*Accipiter nisus*) (Newton 1986). Lethal HEOD levels, found in owls which had other symptoms of organochlorine poisoning, but no evidence for any other cause of death, were in the range 6-44 ppm, with a geometric mean of 14 ppm. That these pesticides may have caused a decline in Barn Owl populations in such regions is supported by survey results. Thus, Prestt (1965) found evidence for a decline in Barn Owl numbers, which was most marked in eastern counties, in the period 1956-1962, following the introduction of heptachlor, aldrin and dieldrin in agriculture. Heptachlor was withdrawn in 1964, and few Barn Owl livers examined after 1966 contained more than 0.5 ppm of residue. But aldrin and dieldrin remained in common use until 1976, after which they were much restricted. All the organochlorines mentioned in this paper were banned completely from 1986, so this source of mortality can be assumed to have disappeared.

The increasing contamination of Barn Owls with second generation rodenticides over the past 15 years was expected from the increasing use of these chemicals, which are gradually replacing warfarin and other first generation rodenticides. In 1993-1994, about one-third of all Barn Owls received contained measurable residues of one or more compounds, but only a small proportion of birds (up to 3 percent of the total) contained residues large enough to have killed them. With yet further increases in usage, however, these chemicals could become a more important cause of mortality in the future.

LITERATURE CITED

Bunn, D.S.; Warburton, A.B.; Wilson, R.D.S. 1982. The Barn Owl. Calton: Poyser.

Cooke, A.S.; Bell, A.A.; Haas, M.B. 1981. Predatory birds, pesticides and pollution. Cambridge: Institute of Terrestrial Ecology.

de Bruijn, O. 1994. Population ecology and conservation of the Barn Owl *Tyto alba* in farmland habitats in Liemers and Achterhoek (The Netherlands). Ardea. 82: 1-109.

DeWitt, J.B.; Menzie, C.M.; Adomaitis, V.A.; Reichell, W.L. 1960. Pesticidal residues in animal tissues. Transactions of North American Wildlife Research Conference. 25: 277-285.

Glue, D.E. 1971. Ringing recovery circumstances of small birds of prey. Bird Study. 18: 137-146.

Hardy, A.R.; Hirons, J.G.; Stanley, P.I. 1982. Relationship of body-weight, fat deposit and moult to the reproductive cycles in wild Tawny Owls and Barn Owls. In: Cooper, J.E.; Greenwood, A., ed. Recent advances in the study of raptor diseases. Keighley: Chiron Publications: 159-163.

Jones, D.M.; Bennett, D.; Elgar, K.E. 1978. Deaths of owls traced to insecticide-treated timber. Nature. 272: 52.

Newton, I. 1986. The Sparrowhawk. Calton: Poyser.

Newton, I.; Bell, A.A.; Wyllie, I. 1982. Mortality of Sparrowhawks and Kestrels. British Birds. 75: 195-204.

Newton, I.; Wyllie, I.; Freestone, P. 1990. Rodenticides in British Barn Owls. Environmental Pollution. 68: 101-117.

Newton, I.; Wyllie, I.; Asher, A. 1991. Mortality causes in British Barn Owls *Tyto alba*, with a discussion of aldrin-dieldrin poisoning. Ibis. 133: 162-169.

Newton, I.; Wyllie, I.; Gray, A.; Eadsforth, C.V. 1994. The toxicity of the rodenticide flocoumafen to Barn Owls and its elimination via pellets. Pesticide Science. 41: 187-193.

Olney, N.J.; Davis, R.P.; Thomas, M.R.; Garthwaite, D.G. 1991a. Rodenticide usage in England on farms growing arable crops 1988. Harpenden: Ministry of Agriculture, Fisheries & Food. Pesticide Usage Survey Report 88.

Olney, N.J.; Davis, R.P.; Thomas, M.R.; Garthwaite, D.G. 1991b. Rodendicide usage on farms in England and Wales growing grassland and fodder crops 1989. Pesticide Usage Surv. Rep. 90. Harpenden: Ministry of Agriculture, Fisheries & Food.

Prestt, I. 1965. An enquiry into the recent breeding status of some of the smaller birds of prey and crows in Britain. Bird Study. 12: 196-221.

Shawyer, C.R. 1987. The Barn Owl in the British Isles. Its past, present and future. London: The Hawk Trust.

Taylor, I.R. 1989. The Barn Owl. Shire: Princes Risborough.

Taylor, I. 1994. Barn Owls. Predator-prey relationships and conservation. Cambridge: University Press.

Territorial and Nesting Behavior in Southern Boobook (*Ninox novaeseelandiae*)

Jerry Olsen and Susan Trost[1]

Abstract.—During 1993-1997, three adjacent nesting pairs of the Southern Boobook (*Ninox novaeseelandiae)* were located and observations made on their behavioral interactions, nests, and young in Canberra, Australia. Territory size was close to 100 ha; not the 4 to 10 ha reported in the literature. Males advertized territorial boundaries with the "*boobook*" call and 'duelled' using this and a "*croaking*" call. Neighboring males entered a rival's territory to challenge the resident male, sometimes near the resident's nest. Both sexes fed the young until 2 to 4 weeks after fledging, when females stopped. Males and their young moved to 'camp out' in various parts of their territories earlier defended.

INTRODUCTION

Southern Boobooks (*Ninox novaeseelandiae)* are the smallest of the nine owl species, five *Tyto* and four *Ninox*, that breed in mainland Australia. Observations on the territorial behavior and vocalizations of these owls have been reported by Fleay (1968), Schodde and Mason (1980), Hollands (1991), Olsen (1994), Shields (1994), and Debus (1996) but none of these studies is based on observations of color-marked birds.

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Southern Boobook (Ninox novaeseelandiae*)*.

During our early observations of Southern Boobooks in Canberra (Olsen and Trost, unpubl. data) we saw an interesting sequence of behaviors—individuals sat close to each other giving "*boobook*" calls followed by a more guttural, breathy "*croaking*" call. Then they made physical contact and gave a *"chittering"* call, like they were fighting. To better understand these observations we studied three pairs in Aranda Bushland across the road from our houses.

METHODS

We found the nest sites of three adjacent owl pairs, color-marked the three males and two of their mates (we couldn't catch one female), and radio-tagged one male. The larger of the pair (by weight) had a brood patch and was determined to be the female. Observations were during a 60-90 minute period, beginning a half hour after sunset. Observations for the three pairs were made during the following timeframes: Pair 1, 30 nights between 3 October 1996 and 3 February 1997; Pair 2, 59 nights between 20 September 1994 and 21 February 1995; Pair 3, 25 nights between 6 October 1993 and 6 March 1994. The period of early October to early February covers the egg stage to post-fledging dispersal. We concentrated our observations on the territorial behavior of the radio-tagged male in 1994-1995; the calls and territorial behavior of Pair 3 in 1993-1994, and the calls and territorial behavior of Pair 1 in 1996-1997.

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RESULTS

Territory Size

Schodde and Mason (1980) reported territory sizes for Southern Boobooks of 8 ha, and Olsen (1994) reported territory sizes of 4 to 10 ha. The radio-tagged male defended, through territorial singing ("*boobook*" calls), an area of about 100 ha. When he had nestlings, the radio-tagged male often roosted during the day some distance from his nest in various parts of his territory.

We saw the adjoining male (Pair 1), who was color-banded, over an area of some 50 ha.

VOCALIZATIONS

Southern Boobook calls are described in Schodde and Mason (1980), Hollands (1991), Olsen (1994) and Debus (1996). The following calls are reported to be given by both sexes: "*Boobook*": the 2-note "*boobook*" call.; "*Croak*": the guttural, repeated "*por-por-por*" that is uttered rapidly and softly; "*Bray*": the vibrating purr, similar to the "*mew*" of an Australian Wood Duck (*Chenotta jubata)*; and "*Trill*": the cricket-like call from nestlings and fledglings. Examples of these calls are on the cassette-tape series by Buckingham and Jackson (1990).

"*Boobook*" Call

We heard one or more of the three males give "*boobook*" calls on most nights we visited the area. The males' call seemed to function as territorial singing, and to communicate with the female, e.g., when he arrived with food. We never confirmed that females give the 2-note "*boobook*" call (table 1), though they did give a single-hoot call.

"*Croak*" Call

We heard the "*croak*" call a number of times, but never confirmed that females gave it. We saw males using this call in a ritual we called 'duelling' (see below). The resident female was often in view when two unidentified owls gave the call, so we believe the call was only given by males (table 1).

"*Bray*" Call

We never confirmed that males used the "*bray*" call. The call seemed to be used by females to solicit food or cooperation from males. If males used the "*boobook*" call near the nest, or as they moved away from the nest, females sometimes used the "*bray*" call in response, never the "*boobook*" call.

"*Trill*" Call

Nestlings and fledglings gave the familiar cricket-like, "*trill*" call described by Fleay (1968). This food-demand call may develop into the adult "*bray*" call. Well after fledging, the young gave this call and we never heard the adults use it, or the fledglings use adult calls. That is, adult females, adult males, and young had three different calls. This contrasts with species like Peregrine Falcons (*Falco peregrinus)* where adult males, females, and young give a 'waik' call that is, or resembles, a food-demand call, and they can all give the familiar "cac-cac" defense call (pers. observ.).

DUELLING

Though Fleay (1968), Schodde and Mason (1980), and Shields (1994) state that Southern Boobooks are not highly territorial, the owls in Aranda Bushland were highly territorial. They frequently sang, using the "*boobook*" call, from

Table 1.—*Number of times we heard (a)* "boobook" *calls by the male or an owl other than the female; (b)* "boobook" *calls by the female; (c)* "bray" *calls by the male; (d)* "bray" *calls by the female; and (e) bouts of* "croaking" *calls:* ***Pair # 1*** *1996-1997 - 30 nights x 1 hour of observation between 3 October 1996 and 3 February 1997 (fledgling period only);* ***Pair # 3*** *1993-1994 - 25 nights x 1.0 hours of observation between 6 October 1993 and 6 March 1994 (nestling and fledgling period)*

Pair	(a)	(b)	(c)	(d)	(e)
#1	37	0	0	1	2
#3	26	0	0	47	6

high perches and, occasionally, participated in 'duelling'.

A typical 'duelling' encounter started when a male called (we believe this was limited to males) and was answered by another. A quiet period followed, then the distant male called again, this time from closer. As the duel progressed, both males gave the "*boobook*" call while 50 m apart on their territorial border. Eventually the two males perched in the same tree, and continued to "*boobook*". This changed to a low, throaty, "*croak*" call. Sometimes there was physical contact, accompanied by a loud "chittering" from one or both participants. What we found strange about this behavior was that the neighboring male crossed over into his rival's territory and challenged him close to its nest with the resident's mate nearby. The female was sometimes silent, or would give "*bray*" calls.

Because this behavior often occurred in the vicinity of a nest site, we can see how some observers might have interpreted it as a 'duet' between a resident male and female. Some of the behavior described by Debus (1996) in mid-October in Jervis Bay National Park was similar to what we observed; he may have heard 'duelling' instead of 'duetting' and copulation.

EXTRA ADULTS

We never saw extra females helping at the nest as suggested by Olsen (1994) but did find an extra adult male apparently foraging and sitting with the fledged nestlings and adult male of Pair 2 two days after the young fledged. The adults of Pair 2 gave no defensive response to this male. When a baited trap was placed under the family group, both adult males came down. The new male was measured (he was smaller than the resident male) and banded, but we did not see him again. Its relationship to the residents was unknown.

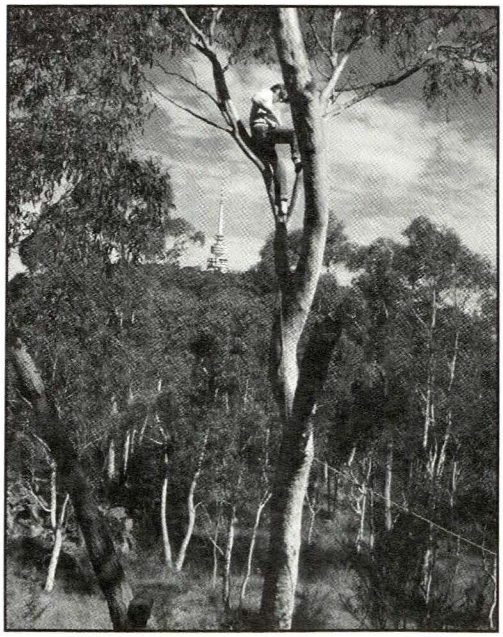
We saw another adult male during daylight in the roost tree normally used by Pair 1 and their fledged young, about 50 m from their nest. The residents were not found on that day. The new male was trapped, measured and marked but was not seen again. He was also smaller than the resident male.

ROOSTING

Adults and young roosted in native cherry (*Exocarpos cupressiformis*), the tops of eucalyptus, and often in hollows. A radio-tagged male (Pair 2) almost always used hollows. While its mate brooded nestlings its most frequently used roost was hollow on the southern border of its territory; a considerable distance and out of view from its own nest at the eastern border of his territory. This roost was within view of the nest of Pair 3 which had eggs. We thought for some time, because it roosted so far from its own nest, that it may have had another mate and family. However, the only interactions we saw or heard were the 'Duels' it apparently had with Male 3. It could easily engage Male 3 in 'Duels' at dusk from this 'favorite' day roost.

POST-FLEDGING DISPERSAL

Young fledged at about 6 weeks old as stated by Fleay (1968) and Schodde and Mason (1980) although Hollands (1991) considered that 6 weeks was too long. Just-fledged young were fed by both parents near the nest and roosted in the nest hollow. After about a week the young could fly well enough to follow the adults further from the nest and 'camp out' with them in various trees for the day. At night, while they followed the adults around from tree to tree, they were defended mainly by the female



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Southern BooBook Owl nest tree.

who would sometimes give a single *"hoot"* or *"yeo"* call and swoop past our heads (males also used these calls but less often). After 2 to 4 weeks, the females at all three territories seemed to 'lose interest' in defending the young and stopped feeding them, although two females still roosted with the family group (table 2). At about this time the young started to follow the males further and further from the nest but the females did not follow. Adult males assumed total responsibility for feeding and defending the fledged young (table 2). Sometimes they gave a single *"hoot"* if we walked too close to the fledglings. Males roosted with fledglings further and further from the nest and 'camped out' in various parts of the territory. After the young and males left, females remained near the nest until we lost contact with them.

One evening, the fledglings from Pair 2 moved into trees near the nest of Pair 3, which contained one nestling, but Male 2 didn't follow. The resident, Pair 3, did not attack or feed the food-demanding fledglings. The Pair 2 fledglings eventually moved back into Male 2's territory.

Male 2's nest was near the eastern border of his territory and he and his fledglings moved away from it, foraged small areas for insects each night, and 'camped out' in a native cherry or eucalypt for the day. Over subsequent nights they continued to move to various locations until they reached the western border of Male 2's territory, about 1.5 kilometers from their nest. The young eventually dispersed from there (table 2).

Table 2.—*Number of days after young fledged that (a) female stopped feeding young, (b) female dispersed, (c) young became independent, (d) young were fed solely by the male:* ***Pair # 1*** *1996-1997 30 nights x 1 hour of observation between 3 October 1996 and 3 February 1997, two young;* ***Pair # 2*** *1994-1995 59 nights x 1.5 hrs of observation between 20 September 1994 and 21 February 1995, three young;* ***Pair # 3*** *1993-1994 25 nights x 1.0 hours of observation between 6 October 1993 and 6 March 1994, one young.*

Pair	(a)	(b)	(c)	(d)
#1	23	34	48	25
#2	25	25	42	17
#3	14	30	43	29

In summary, Male 2 appeared to defend a 100 ha area (through singing and 'duelling') before his young fledged, then lead his fledged nestlings to the eastern, northern, southern, then western border of his territory without their mother. Although they were not radio-tagged, we followed Pairs 1 and 3 each night by listening for the calls of begging young. The adult females of these pairs also stopped feeding their young (table 2) and the adult males also appeared to lead fledglings away from their nest until the young became independent.

DISCUSSION

Territory Size

Reported estimates of territory size are too low because the males in Aranda Bushland defended larger areas.

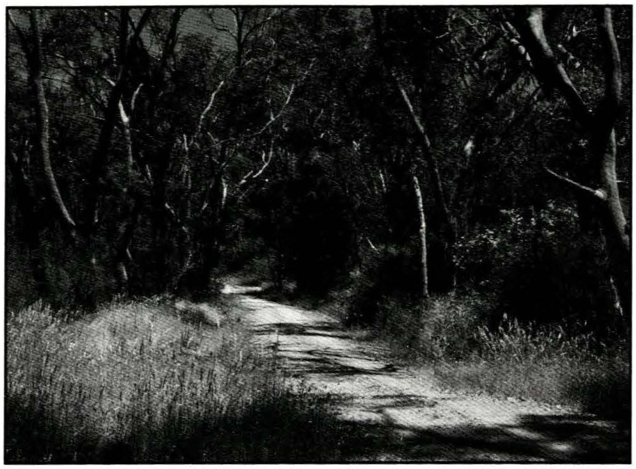
VOCALIZATIONS

"Boobook" and *"Bray"* Calls

It is not clear why we never observed females giving the *"boobook"* call or males giving the *"bray"* call. It may be a characteristic of the three pairs we watched. The *"boobook"* call may be mainly territorial in function with females calling only when they are alone in a territory without a male. The *"bray"* call may be a food-demand call seldom used by males. Also, most of our observations of these owls each year were from around egg-laying to when young dispersed and pairs may engage in 'duets' using the *"boobook"* call earlier (Fleay 1968) or later in the breeding cycle. It is worth noting that, whatever turns out to be typical, these males, females, and young tended to use three quite separate calls as their main vocalizations.

Duelling vs. Duetting

It appears that some of the behaviors interpreted as 'duetting' between mated pairs actually were males 'duelling' with each other, probably over territorial boundaries. More



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Forest habitat of the Southern Boobook Owl.

studies are needed with color-banded birds to determine the nature of 'duetting' in this species, if they duet at all. Duetting could be the male giving a "*boobook*" or "*croak*" call answered by the female's "*bray*" call. Given the difficulties of observing at night, observers could mis-identify individuals, behaviors, and sexes of owls.

'Duelling' was, to us, strange behavior—a neighboring adult male enters its rival's territory and calls, sometimes close to the rival's nest. The behavior probably was antagonistic. But we often wondered if there was some other purpose for the behavior that helped both family groups, a form of communication that established or maintained alliances or status (see below). At least one territorial boundary (between Pairs 1 & 3) changed over the 3 years and it changed near the point where a number of 'duels' took place.

EXTRA MALES

Communication between males was complex. Much of what we saw can be explained by assuming a long-term investment in a territory, where the resident male later led his fledged young. But this does not explain the two adult males seen after the young fledged that were apparently tolerated by both adults. In some birds, like Pied Wagtails (*Motacilla alba)*, the male sometimes shares his territory with a 'satellite', usually a first-winter juvenile or a female from the flock. The cost to the owner is depleted food on the territory but the benefit is that the 'satellite' helps with defense (Davies and Houston 1981). We saw 'extra' males on territories only after the young owls had fledged, so, there was no risk to the territory owner of cuckoldry.

FEMALE MIGRATION

After females stopped feeding the fledglings and left all parental duties to the males, it was not clear how long they remained in the area. It is possible that females fed their young later in the night and we did not see it. But females eventually dispersed, as in other owls, e.g., female Eastern Screech-Owls (*Otus asio)* migrate from their breeding territories during winter (Gehlbach 1994). In other parts of Canberra, we saw pairs of Southern Boobooks roosting together in winter. They could have been mated pairs (females may move to another area to finish their molt, then return) but perhaps they could have been resident males with satellites. If the Aranda Bushland females did not all migrate, and we suspect that some of them did not, their behavior is particularly interesting given Trivers' (1972) theories on parental investment in young.

CONCLUSIONS

These observations differ from previous accounts of the behavior of Southern Boobook and other *Ninox*. Further studies with color-bands and radio-telemetry will show if the behaviors we saw were typical.

ACKNOWLEDGMENTS

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LITERATURE CITED

Buckingham, R.; Jackson, L. 1990. A field guide to Australian bird song, Regent Parrot to Masked Owl. Melbourne, Australia: Bird Observers Club of Australia.

Campbell, B.; Lack, E., eds. 1985. A dictionary of birds. Calton, England: T. & A.D. Poyser. 670 p.

Davies, N.B.; Houston, A.I. 1981. Owners and satellites: the economics of territory defence in the Pied Wagtail, *Motacilla alba*. Journal of Animal Ecology. 50: 157-180.

Debus, S. 1996. Mating behaviour of the Southern Boobook *Ninox novaeseelandiae*. Australian Bird Watcher. 16: 300-301.

Gelbach, F. 1994. The Eastern Screech-owl: life history, ecology, and behavior in the suburbs and countryside. College Station, TX: Texas A&M. 302 p.

Fleay, D. 1968. Nightwatchmen of bush and plain. Milton, Qld.: Jacaranda. 162 p.

Hollands, D. 1991. Birds of the night. Balgowlah, N.S.W.: Reed. 224 p.

Olsen, P. 1994. Southern Boobook. In: Strahan, R., ed. Cuckoos, Nightbirds & Kingfishers of Australia. Pymble, N.S.W.: Angus & Robertson. 130 p.

Schodde, R.; Mason, I. 1980. Nocturnal birds of Australia. Melbourne, Aust.: Lansdowne. 180 p.

Shields, J. 1994. Southern Boobook. In: Strahan, R., ed. Cuckoos, Nightbirds & Kingfishers of Australia. Pymble, N.S.W.: Angus & Robertson. 130 p.

Trivers, R.L. 1972. Parental investment and natural selection. In: Campbell, B., ed, Sexual selection and descent of man. Chicago, IL: Aldine: 136-179.

Landscape Patterns Around Northern Spotted Owl (*Strix occidentalis caurina*) Nest Sites in Oregon's Central Coast Ranges

J.P. Perkins[1], J.A. Thrailkill[1], W.J. Ripple[2], and K.T. Hershey[1]

Abstract.—We investigated landscape characteristics around 41 Northern Spotted Owl (*Strix occidentalis caurina*) nest sites to assess habitat proportions and patterns on this highly fragmented landscape in the central Coast Ranges of Oregon. We compared the proportion of seven forest cover-types between nest sites and random sites at plot sizes of 112 ha, 456 ha, 1,037 ha and 1,844 ha, and fragmentation patterns at the 1,844-ha plot size. Random sites represented available but unused sites. Nest-site selection by Northern Spotted Owls appeared to be influenced by the amount of old-conifer forest around nest sites and the patch size of old-conifer stands where nests were located. Owl nest sites had more old-conifer forest than random sites at all plot sizes ($P \leq 0.058$), but this difference decreased as plot size increased. Old/young forest, consisting of young stands with remnant old trees, was also important as breeding habitat but apparently less than old-conifer forest. The remaining five cover-types were either used in proportion to availability or avoided by owls. We tested for pattern differences in old-conifer forest between nest sites and random sites when the amount of old-conifer forest (habitat) was the same. Most landscape pattern parameters (patch interior, mean patch area, GISfrag, ratio of patch interior to patch area, coefficient of variation of patch area, and perimeter density) did not differ, suggesting that amount and not pattern of habitat is most important for owls when choosing a nest site. Old-conifer forest patches containing nests were larger than random old-conifer patches ($P = 0.050$). We recommend a very conservative approach to timber harvest of remaining old-conifer forests in the region.

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Clutch Size Variation in Tawny Owls (*Strix aluco*) from Adjacent Valley Systems: Can This be Used as a Surrogate to Investigate Temporal and Spatial Variations in Vole Density?

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Abstract.—Research on Tawny Owls (*Strix aluco*) in Kielder Forest, northern England, since 1981 demonstrated that field voles (*Microtus agrestis*) were their most important food. Here, field voles exhibited a 3-4 year cycle of abundance, and mean clutch size in Tawny Owls was significantly related to vole abundance in March. In this analysis we use variations in clutch size as a surrogate to explore whether vole abundance was synchronized over a larger spatial scale, in this case between Kielder Forest and another forest (Kershope) in an adjacent valley system. We show that mean clutch sizes were synchronized between study areas during 1987-1992, but not subsequently (1993-1996). Synchrony was broken in 1993 when voles in Kielder experienced an extended low phase to the cycle resulting in 4 years between peaks, whereas vole cycles in Kershope continued with 3-year periodicity. Thus, since 1993 vole cycles in the two valley systems have been out-of-phase by 1 year. We discuss possible mechanisms whereby vole abundance in nearby areas can oscillate in- and out-of-phase with one another.

In Europe, numerous species of owls feed on rodents with populations that undergo multi-annual fluctuations in abundance (Korpimäki 1992). Owls that are dependent on rodents for food have thus developed numerous strategies to live through food shortages in years when rodents are scarce. Some species are highly mobile, such as Short-eared Owl (*Asio flammeus*) and Snowy Owl (*Nyctea scandiaca*). These owls are able to track changes in rodent abundance over large areas and settle to breed wherever food is most abundant (Korpimäki 1992). Whereas sedentary species, such as Tawny Owl (*Strix aluco*) and Ural Owl (*Strix uralensis)*, remain on territory but cease to breed in poor rodent years (Pietiäinen 1988, Southern 1970). In this paper we concentrate on the Tawny Owl.

The Tawny Owl is a sedentary, nocturnal rodent hunter with its range largely concentrated in the temperate broadleaved forest zone of Europe and Asia. It is replaced by the larger Ural Owl in boreal and alpine conifer forests (Cramp 1985, Lundberg 1980). The Tawny Owl has shown a remarkable flexibility to man-induced changes to European landscapes, having colonized urban habitats (Bevan 1964, Goszczynski *et al.* 1993) and well able to exist in farmland with few trees (Redpath 1995). In Britain, it has readily colonized extensive areas of man-made conifer forest established over the last 75 years, from which Ural owls are absent (Petty and Avery 1990, Petty 1992).

Considering just how abundant the Tawny Owl is in Europe, there is a dearth of studies on its reproduction, compared, for instance, to the vast literature on diet (summarized in Mikkola 1983 and Cramp 1985). Only three studies in Britain have investigated its reproduction in relation to food-supply. Two were in lowland broadleaved woodland near Oxford, southern England where bank voles (*Clethrionomys glareolus*) and woodland mice (*Apodemus sylvaticus* and *A. flavicollis*) were the main prey (Hirons 1976, Southern 1970), and the third was on farmland in Aberdeenshire, northern Scotland, where field voles (*Microtus agrestis*) were more important (Hardy 1977, Hardy 1992).

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There has been much recent interest in the causes and consequences of multi-annual cycles of microtine rodents in Scandinavia (Hanski *et al.* 1991, Hanski and Henttonen 1996, Hansson and Henttonen 1985). This has been largely concerned with temporal patterns, but more recently with spatial aspects (Steen *et al.* 1996). Few studies have been designed to investigate the spatial dynamics of multi-annual rodent cycles, but the literature generally indicates that vole cycles are synchronized over large geographical areas (Hanski *et al.* 1991). So, vole-dependent predators suffer either heavy mortality in trough years between cycle peaks unless other prey are available, or they are highly mobile and "track" high vole densities, and may thus have a synchronizing effect on vole abundance over large areas (Ims and Steen 1990; Korpimäki 1986, 1992; Norrdahl and Korpimäki 1996; Ydenberg 1987).

More recently, Petty (1992) has investigated how Tawny Owls have adapted to man-made conifer forests in northern England. Here the owls fed largely on field voles, which were most abundant on clearcuts, and all demographic measurements of the owl population were significantly related to vole abundance. Vole abundance fluctuated on a 3-year cycle but with some spatial asynchrony. This meant that at any one time, vole numbers could be declining in some parts of the forest while increasing in others. In this analysis, we use clutch size variation in Tawny Owls as a surrogate to investigate if vole abundance was synchronized over a larger spatial scale, in this case adjacent valley systems that straddle the border between England and Scotland.

MATERIALS AND METHODS

Study Areas

The two study areas, in Kielder and Kershope Forests, are situated in the border area between England and Scotland (fig. 1). These forests lie in adjacent valley systems separated by a higher area of treeless moorland, and form part of a much larger area of man-made conifer forest planted over the last 70 years. The forest in both areas comprise largely Sitka spruce (*Picea sitchensis)* and Norway spruce (*Picea abies)* managed on a clearcutting system (40-60 year rotation length), which over the last 25 years has created a mosaic of different-aged stands of trees in older parts of each forest (Petty *et al.* 1995). Clearcuts ranged in size from 5 ha to more than 100 ha, with the smallest in valley bottoms. The current clearcutting program in Kielder Forest District, which included both our study areas, is around 1,000 ha per year. The center of the Kielder study area (55°13′ N, 2°33′ W) was 17.7 km NE of the center of the Kershope study area (55°08′ N, 2°47′ W). The main differences between study areas were that Kielder was higher and

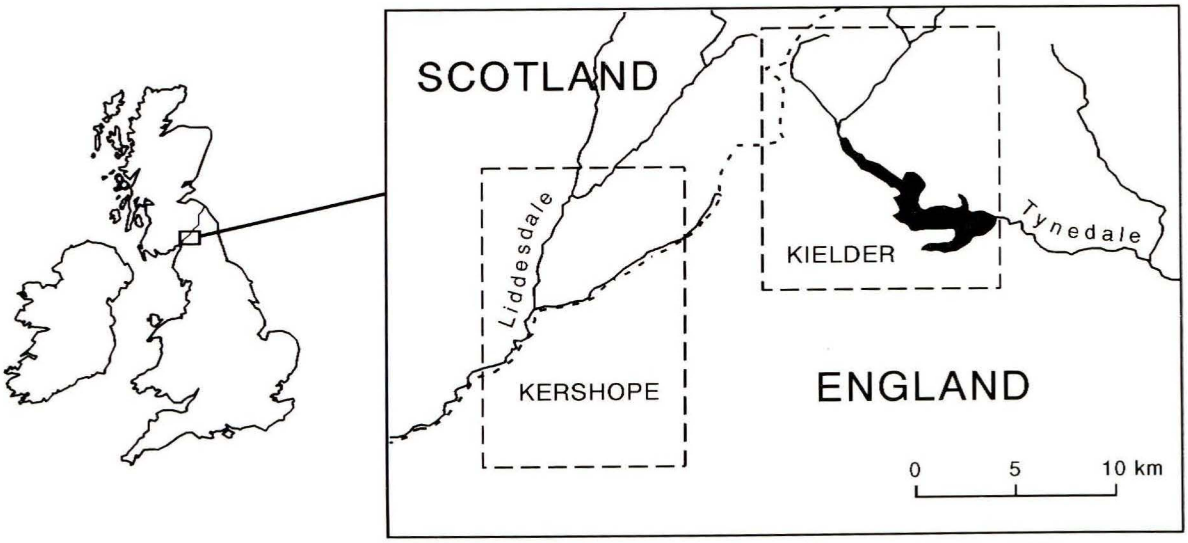

Figure 1.—*Location of the Kielder (180 km²) and Kershope (170 km²) study areas in the border area between England and Scotland. The study areas were defined by the smallest rectangle that included all Tawny Owl nest sites based on 1 km square of the national grid. Not all ground in each study area was monitored for Tawny Owls.*

contained more forest than Kershope. In Kershope, over 50 percent of the study area was farmland (mainly grass pasture) and moorland, compared to less than 25 percent in Kielder which was mostly heather (*Calluna vulgaris*) moorland.

Tawny Owl Numbers and Breeding Performance

Nest Visits and Number of Pairs Used in the Analysis

Within both study areas, owls bred largely in nest boxes provided for them (Petty 1987, Petty *et al.* 1994). Checks of potential nest sites (nest boxes and natural sites) commenced in March, with subsequent visits timed to obtain the data required with the minimum of disturbance. In Kershope we had no data on the number of territorial pairs present each year, just those that laid. Petty (1992) showed that, in Kielder, the percentage of the territorial population that laid varied from 84-96 percent in years when voles were abundant to less than 30 percent in the trough years between vole cycles (see below). Therefore, the sample used in this analysis is based on the number of pairs that laid at least one egg. This amounted to 565 clutches from Kielder during 1981-1996 and 187 clutches from Kershope during 1987-1996 (table 1).

Table 1.—*Number of Tawny Owl (*Strix aluco*) pairs laying at least one egg in the Kieder and Kershope Forests along the border area between England and Scotland.*

Year	Kielder	Kershope
1981	41	-
1982	34	-
1983	10	-
1984	43	-
1985	44	-
1986	4	-
1987	48	20
1988	50	19
1989	14	5
1990	51	23
1991	63	25
1992	22	1
1993	27	29
1994	50	27
1995	35	6
1996	29	32
Total	**565**	**187**

Clutch Size

On the first visit to a nest with eggs, each egg was marked with a unique code using a black spirit-based felt-tip pen. Egg lengths (l) and breadths (b) (at the widest point) were measured to the nearest 0.01 cm with plastic dial calipers. Each egg was weighed (W) in a small polythene bag with a 50 g pesola balance, to the nearest 0.1 g. A density index (DI) was calculated for each egg when DI = W/(0.507*b *l) (Petty 1992). The DI decreases through incubation as eggs lose weight (Furness and Furness 1981). Any clutch with a DI for any egg of > 1.060 could have been incomplete, so was revisited to obtain the complete clutch. Clutches where all eggs had a DI < 1.059 were considered to be complete. Most Tawny Owls laid from mid-March to mid-April (Petty 1992).

There were no predators in either study area, such as pine martens (*Martes martes*), that could remove eggs from owl nests in boxes or elevated natural sites. Foxes (*Vulpes vulpes*) were potential predators of ground nests, but only two such nests were found once nest boxes had been provided, and neither were predated (Petty *et al.* 1994). Red squirrels (*Sciurus vulgaris)* were present in both study areas, and were considered capable of removing eggs from nests but this was never recorded. Squirrels occasionally built dreys on top of deserted owl eggs, but eggs always remained unbroken.

Nest Desertions Due to Observer Disturbance

Some female owls deserted complete or incomplete clutches following observer visits (Kielder 1981-1996, n = 66; Kershope 1987-1996, n = 10). Most desertions followed the first visit to the nest (Petty 1992). Desertion during egg-laying often resulted in the clutch being continued without interruption at another nest site within the territory. Of the females which deserted after incubation commenced, about half laid a second clutch at a new nest site, but after an interval much longer than normal between eggs. Generally the more advanced the nesting cycle when the failure occurred, the less the chance of a relay. Pairs which failed with chicks older than 6 days never relaid. Virtually all repeat clutches were considered to result from first-clutch desertions caused by the observer. Therefore, to avoid using two or more clutches from the same female in a year, the following procedure removed these observer effects. Incomplete and complete clutches that were deserted were excluded and substituted by the replacement clutch. There was no significant difference between completed first and repeat clutch sizes (Petty 1992). When deserted first clutches were not replaced, or when these were replaced and subsequently failed, then clutch size from the first clutch was used.

Tawny Owl Diet

In Kielder Forest, field voles were the main prey of Tawny Owls (Petty 1989, 1992). Field voles comprised 72 percent of 2,429 prey items found in pellets collected at roost sites during 1980-1989, and 66 percent of 991 prey items identified in owl nests during the same period. We have no comparable data from Kershope, but field voles were the most frequent prey in owl nests.

Estimating Field Vole Abundance

A Vole Sign Index (VSI) was used to estimate the abundance of field voles on clearcuts throughout the Kielder study area. The VSIs were done on around 20 grass-dominated sites in March from 1985 until 1996. At each site, a 25 cm^2 quadrat was thrown 25 times along a similar route, and the presence or absence of fresh (green) grass clipping in vole runs recorded. Thus calculated, the VSI for each site ranged from 0 to 25. In this analysis we use the mean VSI value from all sites. The accuracy of this method for assessing vole abundance had previously been checked by trapping voles on one vole sign assessment site, at the same time that the VSI was done in March during 1985-1990, to provide a vole trapping index (VTI) (Petty 1992). The VTI was equivalent to the number of voles caught per 100 snap trap nights. Each trapping session comprises 576 trap nights. There was a significant relationship between the VSI and VTI in March (fig. 2).

RESULTS

Relationship Between Vole Abundance and Clutch Size

In Kielder during 1985-1996, 77 percent of variation in clutch size of Tawny Owls was accounted for by the March VSI (fig. 3). Thus, a comparison of annual mean clutch sizes in Tawny Owls in Kielder and Kershope should reflect variation in vole abundance between study areas in March.

Clutch Size Variation Between Study Areas

The longer-term data set on mean clutch sizes from Kielder indicated regular 3-year vole

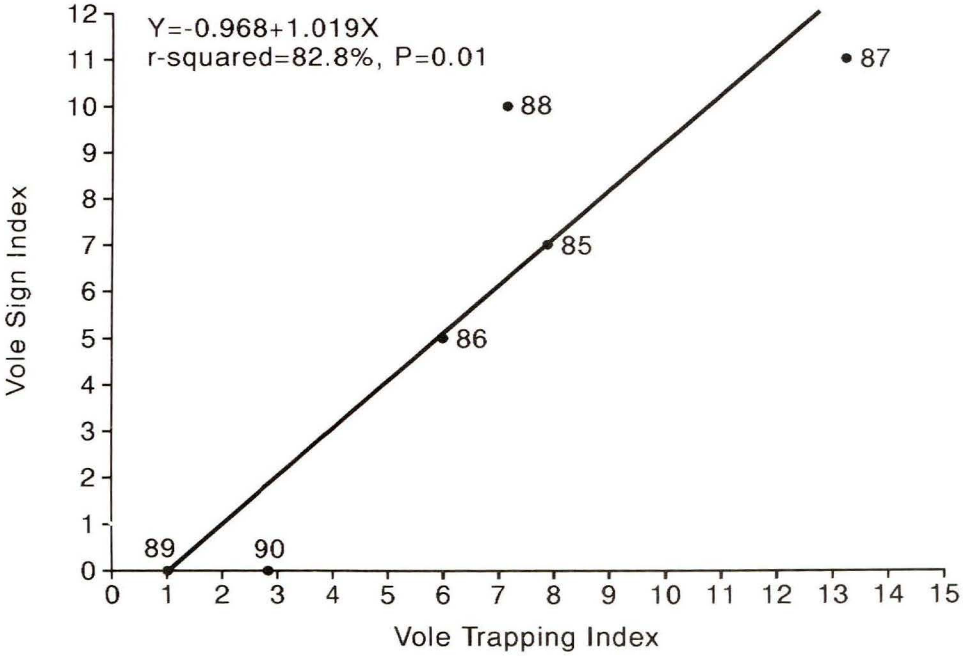

Figure 2.—*The relationship between the Vole Trapping Index and the Vole Sign Index in March in the Kielder study area in the border area between England and Scotland.*

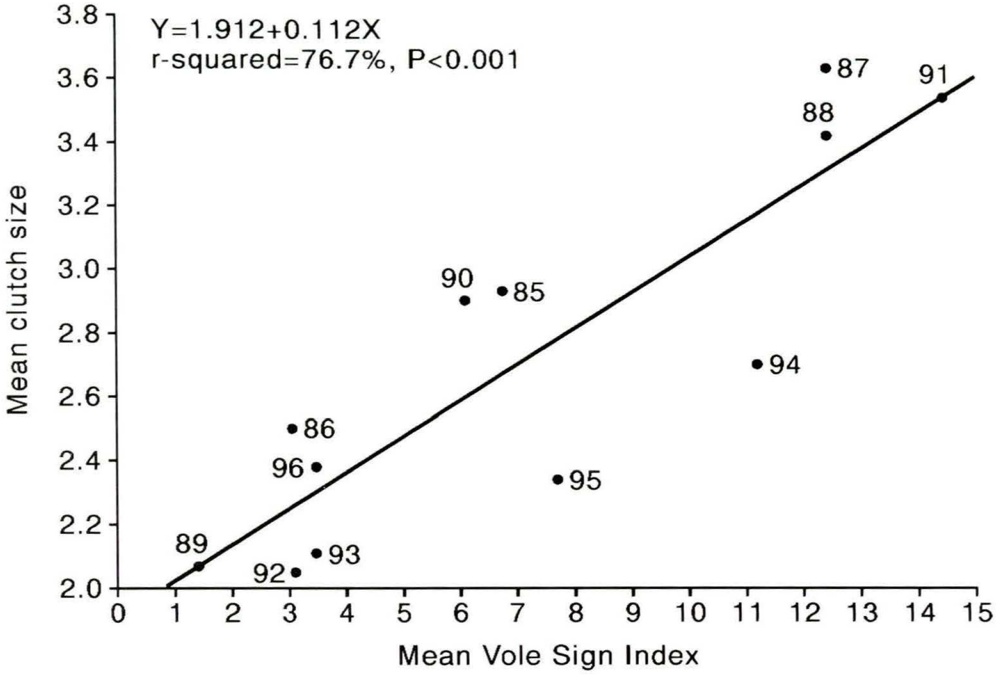

Figure 3.—*Relationship between the mean Vole Sign Index in March and mean clutch size in Tawny Owls (*Strix aluco*) in the Kielder study area in the border area between England and Scotland.*

cycles from 1981 until 1992, with trough years in 1983, 1986, 1989, and 1992, and higher clutch sizes in intervening years (fig. 4). The Kershope data started in 1987, and from then until 1992 it tracked clutch size variation of Tawny Owls in Kielder (r = 0.85, df = 5, P = 0.03), but not during 1993-1996 (r = -0.30, df = 3, P = 0.70). Since 1992, the data from Kershope indicated that vole abundance continued to cycle at 3-year periodicity with high amplitude. Whereas in Kielder the overall amplitude declined, with both lower peaks and

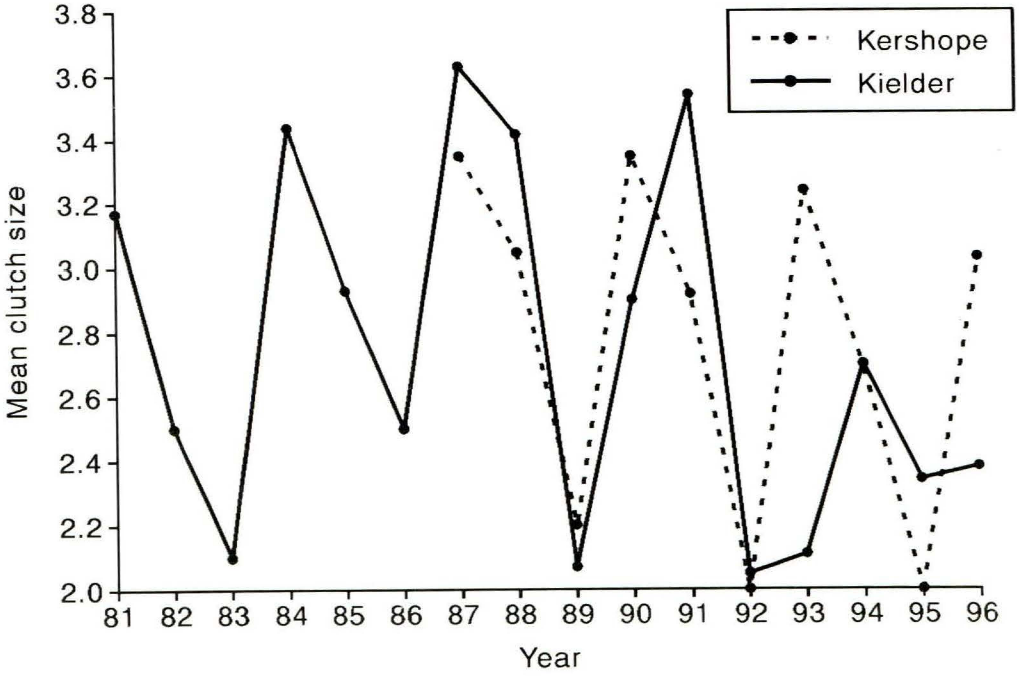

Figure 4.—*Annual variation in mean clutch size of Tawny Owls (*Strix aluco*) in the Kielder(1981-1996) and Kershope (1987-1996) study areas in the border area between England and Scotland.*

higher troughs, and the 1992 trough extended into 1993, resulting in the study areas being out-of-phase by one year since 1993.

Clutch Size Variation in Relation to Vole Abundance

Excluding the years 1993-1996 in Kielder, a typical 3-year vole cycle in our study areas comprised: (1) a spring when vole numbers were low (low phase), before starting to increase in late summer, but after the owls breeding season; (2) a spring with vole numbers continuing to increase (increasing phase); (3) a spring when voles declined from a winter peak (declining phase). In four out of five cycles in Kielder and all three cycles in Kershope, clutch sizes peaked in the increasing phase and declined in the following year (fig. 4).

There was little difference between study areas in mean clutch size in each of these "vole year classes" (fig. 5). Median clutch sizes were similar in Kielder and Kershope in the low and increasing phases of the vole cycle (low phase, Mann-Whitney, Z = 0.16, P = 0.88; increasing phase, Mann-Whitney, Z = 0.57, P = 0.57), but were significantly higher in the declining phase in Kielder than in Kershope (Mann-Whitney, Z = 2.47, P = 0.01). In both study areas the modal clutch size was three in increasing and declining years and two in low years.

DISCUSSION

Hanski *et al.* (1991) indicated that in Fennoscandia, vole cycles decreased in periodicity from around 5-year intervals at 70°N to 3-year intervals at 56-60°N, with no clear evidence of multi-annual cycles further south. The amplitude of the cycles also showed a declining gradient from north to south. Hanski *et al.* (1991) also explored the role of predators in vole cycles and concluded that their results were consistent with the hypothesis that cycles were driven by specialist predators, and that generalist predators could modify cycles. Other studies indicated that a lack of multi-annual cycles in rodent populations in Southern Sweden could be the result of predation (Erlinge 1987; Erlinge *et al.* 1983, 1984, 1988). In such fragmented habitats, generalist predators were abundant. These fed on alternative prey when voles were scarce, but increased their predation on voles once voles started to increase, to the point where numbers then decreased. In this way they kept voles at a fairly stable level and so prevented the development of multi-annual cycles. In contrast, in northern Scandinavia with pronounced 3-5 year vole cycles,

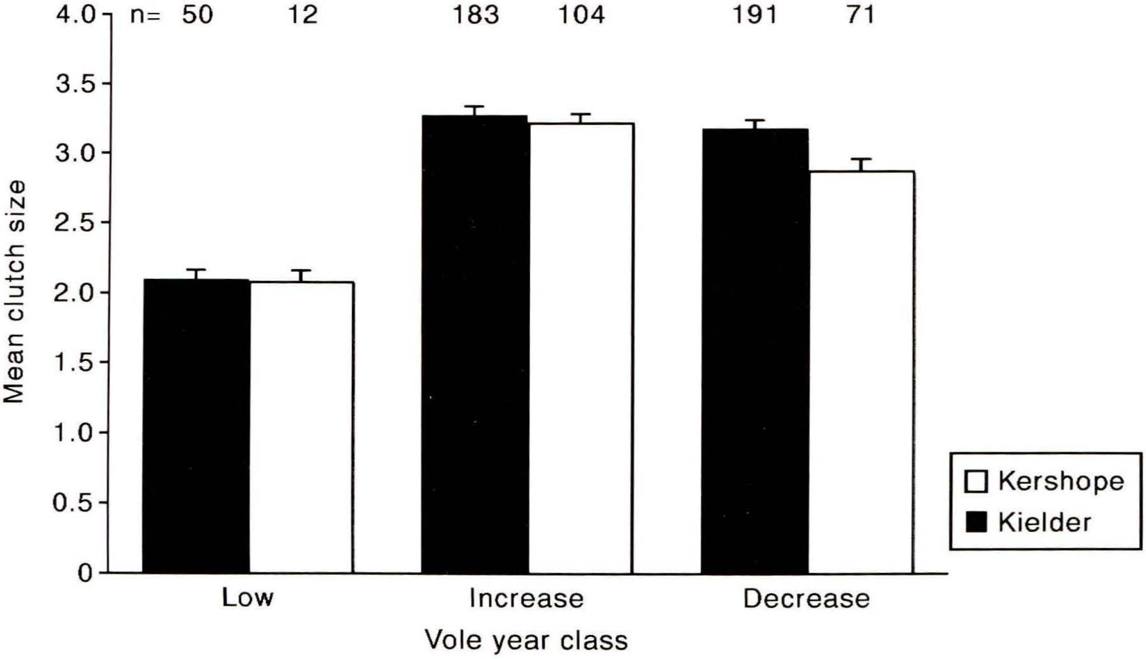

Figure 5.—*Comparison of mean clutch sizes (with SE bars) of Tawny Owls* (Strix aluco) *between the Kielder and Kershope study area, in the border area between England and Scotland, in three vole year classes that typify one vole cycle.*

generalist predators were scarce or absent, and vole numbers were able to increase rapidly from the low point in the cycle, because there was little predation to delay an increase in numbers (Hanski *et al.* 1991; Korpimäki 1985, 1986; Korpimäki and Norrdahl 1991). Only when voles became abundant did specialist predators (mainly mustelids and nomadic owls) start to exploit them and reduce numbers.

The temporal trends in vole abundance identified from our analyses indicated cycle lengths of 3 years, which at 55°N was similar to that from cyclic populations at 56-60°N in southern Fennoscandia. However, the most interesting aspect to emerge from our study was that vole cycles in adjacent valley systems oscillated in- and out-of-phase with each other. There was also some indication that the amplitude of cycles in Kielder had reduced, due to increasing local asynchrony[2]. Thus, within the same valley system, it appears possible for vole population in different patches to switch between synchronous and asynchronous fluctuations. So, what causal factor(s) from the current batch of hypotheses could explain these phenomena?

First though, it is easier to reject hypotheses that cannot explain the pattern of cyclicity we have reported. In our study areas, generalist predators such as badger (*Meles meles*), Buzzard (*Buteo buteo*) (in Kershope only), fox, mink (*Mustela vison*), stoat (*Mustela erminea*) and Tawny Owl were far more abundant than specialist avian vole predators such as Long-eared Owl (*Asio otus*), Short-eared Owl, and Kestrel (*Falco tinnunculus*). We suspect the weasel (*Mustela nivalis*) was abundant, but we have no data on its density or distribution. Therefore, from the predator assemblages present in our study areas which comprised mostly generalists, the prediction from the predator hypothesis would be that our vole population should be non-cyclic, but this was not the case.

Most species of predator present in both study areas were relatively sedentary. So, there were unlikely to be movements between study areas. For instance, many Tawny Owl chicks have been ringed in both study areas over the course of the study, but none have been recovered as breeding adults in a different study area to that in which they were ringed (Petty 1992). Thus, voles and their predators in the two study areas were largely independent of each other. If this was the case, then why were cycles in Kershope and Kielder in-phase for part of the study (1987-1992), unless just by chance?

Nor can any of the weather/climate-related hypotheses explain our observations (Hansson and Henttonen 1985). Weather patterns are unlikely to vary over such a small spatial scale, so if weather was a causal factor, then vole abundance should have been synchronized between valleys.

So, what could explain our observations? The key may lie in trying to understand why the pattern of multi-annual cycles appears to have changed since 1993 in Kielder but not in Kershope. Our approach has been to try and identify any habitat differences between valleys that may explain this change.

Both valleys have large areas of man-made spruce forest where patch clearcutting is now widespread. Clearcuts provide the most important vole habitat within each forest, particularly on surface water gley soils in valley bottoms and on lower slopes. On these sites, grassy vegetation, dominated by *Deschampsia caespitosa*, develops within 1-3 years of clearcutting, and then remains suitable for voles until the new tree crop starts to shade out the ground vegetation, from 12-15 years after replanting (Petty 1992). Clearcuts at higher elevation are usually on peaty gley soils or blanket peats where re-colonization by vegetation is slower and often dominated by *Calluna vulgaris*. Such sites provide poorer habitat for field voles. Clearcuts are usually separated from each other by closed-canopy stands of close-grown spruce with little ground vegetation apart from bryophytes. So, they provide islands of vole habitat within a larger matrix of unsuitable habitat (spruce forest).

During the early part of our study in Kielder, most clearcutting was in the older forest at lower elevations, and these were on soil types that produced the best vole habitat. Recently, the pattern of clearcutting has altered the configuration of habitat mosaics at the landscape scale, with less clearcutting at lower elevations and more on the upper slopes and watersheds. So, the gross amount of good vole habitat may have declined, and it may also have become more patchily distributed. This corresponds to: (1) a change in the territorial population of Tawny Owls, from 44 pairs in 1981, to a peak of 66 pairs in 1991, followed by a decline to 54 pairs in 1996[3] (Petty 1992); and (2) declining synchrony in vole abundance within Kielder. Whereas in Kershope, there are still numerous large clearcuts suitable for voles, and unlike Kielder, the forest is in closer contact with extensive areas of farmland (unimproved or improved pasture) where voles are abundant and cycles synchronized.

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Jansen (1995) has recently shown from modeling that patch dynamics may have an important influence on population fluctuations. For example, prey populations in small patches were more likely to fluctuate asynchronously than prey in large patches, and fluctuations in small patches were able to flip in- and out-of-phase with each other. This generates a pronounced cycle during an in-phase oscillation, but the amplitude is dampened during an out-of-phase oscillation. There are analogies here with changes that have occurred in Kielder, in both patterns of clearcutting and in the periodicity and amplitude of vole cycles.

Steen *et al.* (1996) studied spatio-temporal patterns in bank vole population cycles in Norway, and concluded that these were not related to habitat. However, from our results we feel that the scale and distribution of habitat have crucial influences on rodent population fluctuations. This hypothesis does not of course rule out other factors. For instance, habitat quality, predation, and intrinsic factors within rodent populations, may help to shape the pattern of population fluctuations, but in a proximate rather than ultimate manner. There are two predictions from our hypothesis. First, synchronized multi-annual cycles should occur only in suitable large-scale habitats (large patches). Suitability of the habitat being very important, for instance, heavy grazing can operate as a proximate factor to dampen synchronized multi-annual cycles in otherwise suitable habitat. Such a process has frequently been observed when heavily-grazed grasslands in the British uplands are converted over a short period of time into extensive conifer forests. Prior to afforestation, rodents populations are non-cyclic and occur at low density (Charles 1981). Domestic stock are then excluded by fencing prior to tree planting, grass growth recovers and field vole numbers dramatically increase to generate 1-3 multi-annual cycles before tree growth makes the habitat again unsuitable (Charles 1956, Chitty 1952, Goddard 1935, Lockie 1955, Petty 1996, Petty and Avery 1990). Second, overall synchrony in multi-annual cycles should break down in fragmented habitats (small patches) because; either individual patches are out-of-phase with each other, even though cycles are still multi-annual, or cycles become annual with rodent numbers increasing from spring to autumn because over-winter predation (acting as a proximate factor) reduces numbers to a low point by the following spring.

Our results indicate that clutch size variation in Tawny Owls can be used to investigate not only temporal but also spatial variations in vole abundance. It is often laborious to obtain estimates of vole abundance at the same time from trapping or vole signs indices at a landscape scale or regional scale. Therefore, future comparisons of breeding performance of vole-eating raptors appear to offer a promising method to explore more fully the spatial dynamics of multi-annual rodent cycles.

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LITERATURE CITED

Bevan, G. 1964. The food of Tawny Owls in London. London Bird Report. 29: 56-72.

Charles, N.W. 1956. The effect of a vole plague in the Carron Valley, Stirlingshire. Scottish Forestry. 10: 201-204.

Charles, N.W. 1981. Abundance of the field vole (*Microtus agrestis*) in conifer plantations. In: Forest and woodland ecology. Cambridge: Institute of Terrestrial Ecology: 135-137.

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[3] S.J. Petty, address as in footnote 1, unpublished data.

Chitty, D. 1952. Mortality amongst voles (*Microtus agrestis*) at Lake Vyrnwy, Montgomeryshire in 1936-1939. Philosophical Transactions of the Royal Society of London B. 236: 505-552.

Cramp, S., ed. 1985. The birds of the western Palearctic, Volume 4. Oxford: Oxford University Press. 960 p.

Erlinge, S. 1987. Predation and noncyclicity in a microtine population in southern Sweden. Oikos. 50: 347-352.

Erlinge, S.; Göransson, G.; Hansson, L.; Högstedt, G.H.; Liberg, O.; Nilsson, I.N.; Nilsson, T.; Schantz, T.von; Sylven, M. 1983. Predation as a regulatory factor on small rodent populations in southern Sweden. Oikos. 40: 36-52.

Erlinge, S.; Göransson, G.; Högstedt, G.; Jansson, G.; Liberg, O.; Lomon, J.; Nilsson, I.N.; Schantz, T.von; Sylven, M. 1984. Can vertebrate predators regulate their prey. American Naturalist. 123: 125-133.

Erlinge, S.; Liberg, O.; Göransson, G.; Lomon, J.; Högstedt, G.; Nilsson, I.N.; Jansson, G.; Schantz, T.von; Sylven, M. 1988. More thoughts on vertebrate predators regulation of prey. American Naturalist. 132: 148-154.

Furness, R.W.; Furness, B.L. 1981. A technique for estimating the hatching dates of eggs of unknown laying dates. Ibis. 123: 98-123.

Goddard, T.R. 1935. A census of Short-eared Owls (*Asio f. flammeus*) at Newcastleton Forest, Roxburghshire, 1934. Journal of Animal Ecology. 4: 113-118, 289-290.

Goszczynski, J.; Jablonski, P.; Lesinski, G.; Romanowski, J. 1993. Variation in diet of Tawny Owl *Strix aluco* L. along an urbanization gradient. Acta Ornithologica. 27: 113-123.

Hanski, I.; Henttonen, H. 1996. Predation on competing rodent species: a simple explanation of complex patterns. Journal of Animal Ecology. 65: 220-232.

Hanski, I.; Hansson, L.; Henttonen, H. 1991. Specialist predators, generalist predators and the microtine rodent cycle. Journal of Animal Ecology. 60: 353-367.

Hansson, L.; Henttonen, H. 1985. Gradients in density variation of small rodents: the importance of latitude and snow cover. Oecologia 67: 394-402.

Hardy, A.R. 1977. Hunting ranges and feeding ecology of owls in farmland. Aberdeen: University of Aberdeen. Ph. D. thesis.

Hardy, A.R. 1992. Habitat use by farmland Tawny Owls *Strix aluco*. In: The ecology and conservation of European owls. Peterborough: Joint Nature Conservation Committee (UK Nature Conservation, No. 5): 55-63.

Hirons, G.J.M. 1976. A population study of the Tawny Owl *Strix aluco* L. and its main prey in woodland. Oxford: University of Oxford. 222 p. Ph.D. dissertation.

Ims, R.A; Steen, H. 1990. Geographical synchrony in Microtine population cycles: a theoretical evaluation of the role of nomadic avian predators. Oikos. 57-381-387.

Jansen, V.A.A. 1995. Regulation of predator-prey systems through spatial interaction: a possible solution to the paradox of enrichment. Oikos. 74: 384-390.

Korpimäki, E. 1985. Rapid tracking of microtine populations by avian predators: possible evidence for stabilizing predation. Oikos. 45: 21-30.

Korpimäki, E. 1986. Predation causing synchronous decline phases in microtine and shrew populations in western Finland. Oikos. 46: 124-127.

Korpimäki, E. 1992. Population dynamics of Fennoscandian owls in relation to wintering conditions and between-year fluctuations of food. In: The ecology and conservation of European owls. Peterborough: Joint Nature Conservation Committee (UK Nature Conservation, No. 5): 1-10.

Korpimäki, E.; Norrdahl, K. 1991. Do breeding nomadic avian predators dampen population fluctuations of small mammals? Oikos. 62: 195-208.

Lockie, J. 1955. The breeding habits of Short-eared Owls after a vole plague. Bird Study. 2: 53-69.

Lundberg, A. 1980. Why are the Ural Owl *Strix uralensis* and the Tawny Owl *Strix aluco* parapatric in Scandinavia. Ornis Scandinavica. 11: 116-120.

Mikkola, H. 1983. Owls of Europe. Calton: Poyser. 397 p.

Norrdahl, K.; Korpimäki, E. 1996. Do nomadic avian predators synchronise population fluctuations of small mammals? A field experiment. Oecologia (in press).

Petty, S.J. 1987. The design and use of a nestbox for Tawny Owls *Strix aluco* in upland forests. Quarterly Journal of Forestry. 81: 103-109.

Petty, S.J. 1989. Productivity and density of Tawny Owls *Strix aluco* in relation to the structure of a British spruce forest. Annales Zoologici Fennici. 26: 227-233.

Petty, S.J. 1992. Ecology of the Tawny Owl *Strix aluco* in the spruce forests of Northumber-land and Argyll. Milton Keynes: The Open University. 295 p. Ph.D. dissertation.

Petty, S.J. 1996. Adaptations of raptors to man-made spruce forests in the uplands of Britain. In: Raptors in human landscapes. London: Academic Press: 201-214.

Petty, S.J; Avery, M.I. 1990. Forest bird communities. For. Comm. Occas. Pap. 26. Edinburgh: Forestry Commission. 110 p.

Petty, S.J.; Garson, P.J.; McIntosh, R., eds. 1995. Kielder - the ecology of a man-made spruce forest. Forest Ecology and Management. 79: 1-160.

Petty, S.J.; Shaw, G.; Anderson, D.I.K. 1994. Value of nest boxes for population studies of owls in coniferous forest in Britain. Journal of Raptor Research. 28: 134-142.

Pietiäinen, H. 1988. Reproductive tactics of the Ural Owl *Strix uralensis* depending on cyclic vole populations. Helsinski: University of Helsinski. Ph.D. dissertation.

Redpath, S.M. 1995. Habitat fragmentation and the individual: Tawny Owls *Strix aluco* in woodland patches. Journal of Animal Ecology. 64: 652-661.

Southern, H.N. 1970. The natural control of a population of Tawny Owls (*Strix aluco*). Journal of Zoology, London. 162: 197-285.

Steen, H.; Ims, R.A.; Sonerud, G.A. 1996. Spatial and temporal patterns of small-rodent population dynamics at a regional scale. Ecology. 77: 2365-2372.

Ydenberg, R.C. 1987. Nomadic predators and geographical synchrony in microtine cycles. Oikos. 50: 270-272.

Nest Sites and Reproductive Success of Barred Owls (*Strix varia*) in Michigan

Sergej Postupalsky[1], Joseph M. Papp[2], and Lewis Scheller[3]

Abstract.—During 1976-1995 we monitored 114 Barred Owl (*Strix varia*) breeding attempts in northern Michigan. We describe nest sites and report reproductive success for different types of nest sites. Most natural nest sites were tree cavities caused by decay at places where a limb or tree top had broken off. The mean d.b.h. of cavity trees (N = 18) was 48 cm and mean cavity floor area (N = 19) 508 cm^2. Overall, 75 percent of breeding attempts were successful with a mean brood size (N = 75) of 1.97 young/productive nest. Owls nesting in tree cavities (N = 49) and in boxes (N = 52) showed similar productivities. While 80 percent of nests in cavities and boxes combined were productive with mean brood size (N = 81) of 2.01 young/productive nest, only 31 percent of breeding attempts in hawk nests and other open sites (N = 13) were successful with mean brood size (N = 3) of 1.0 young/productive nest. Owlets falling from open nests prematurely, before they were able to climb, is seen as the principal cause of poor productivity. The critical importance to Barred Owls of large trees and snags with cavities is emphasized in their management.

Among the five species of large owls which breed in North America, the Barred Owl (*Strix varia*) is the least well studied. Early accounts of its life history (Bent 1938) include some qualitative information on nest sites and habitat, anecdotal observations of behavior, good data on clutch size, but nothing on breeding success. Most ornithologists at that time were egg collectors and thus a study of "nesting habits" usually ended with the discovery of the nest and collection of the clutch. Following the introduction of nonlethal techniques by Errington (1930, 1932a), food habits studies were in the forefront during the ensuing decades (Errington 1932b, Errington and McDonald 1937, Hamerstrom and Hamerstrom 1951, Korschgen and Stuart 1972, Mendall 1944, Wilson 1938).

Most recent research involving Barred Owls has concerned habitat use, territoriality, relationships with the Great Horned Owl (*Bubo virginianus*) (Bosakowski 1994, Bosakowski *et al.* 1987, Devereaux and Mosher 1984, Elody and Sloan 1985, Fuller 1979, Laidig and Dobkin 1995, McGarigal and Fraser 1984, Nicholls and Fuller 1987, Nicholls and Warner 1972, Yannielli 1991), and range expansion into the Pacific Northwest (Dunbar *et al.* 1991, Hamer *et al.* 1994, Taylor and Forsman 1976). The population dynamics of this widespread and still at least locally common species have not been studied at all and even such basic information as mortality and reproductive rates remain unavailable. The only information on Barred Owl reproductive success we found in the literature is in the papers by Devereaux and Mosher (1984), Dunstan and Sample (1972), and Johnson (1987).

Our objectives were (1) to describe Barred Owl nest sites and cavity trees to determine the range of cavity and tree sizes these owls require for nesting, and (2) to determine reproductive success for nests in tree cavities, nest boxes, and open nests.

STUDY AREA AND METHODS

Study Area

Most observations were from two study areas in Alpena County in the northeastern Lower Peninsula of Michigan (fig. 1). The easterly area, approximately 28 km^2, was located 11 km

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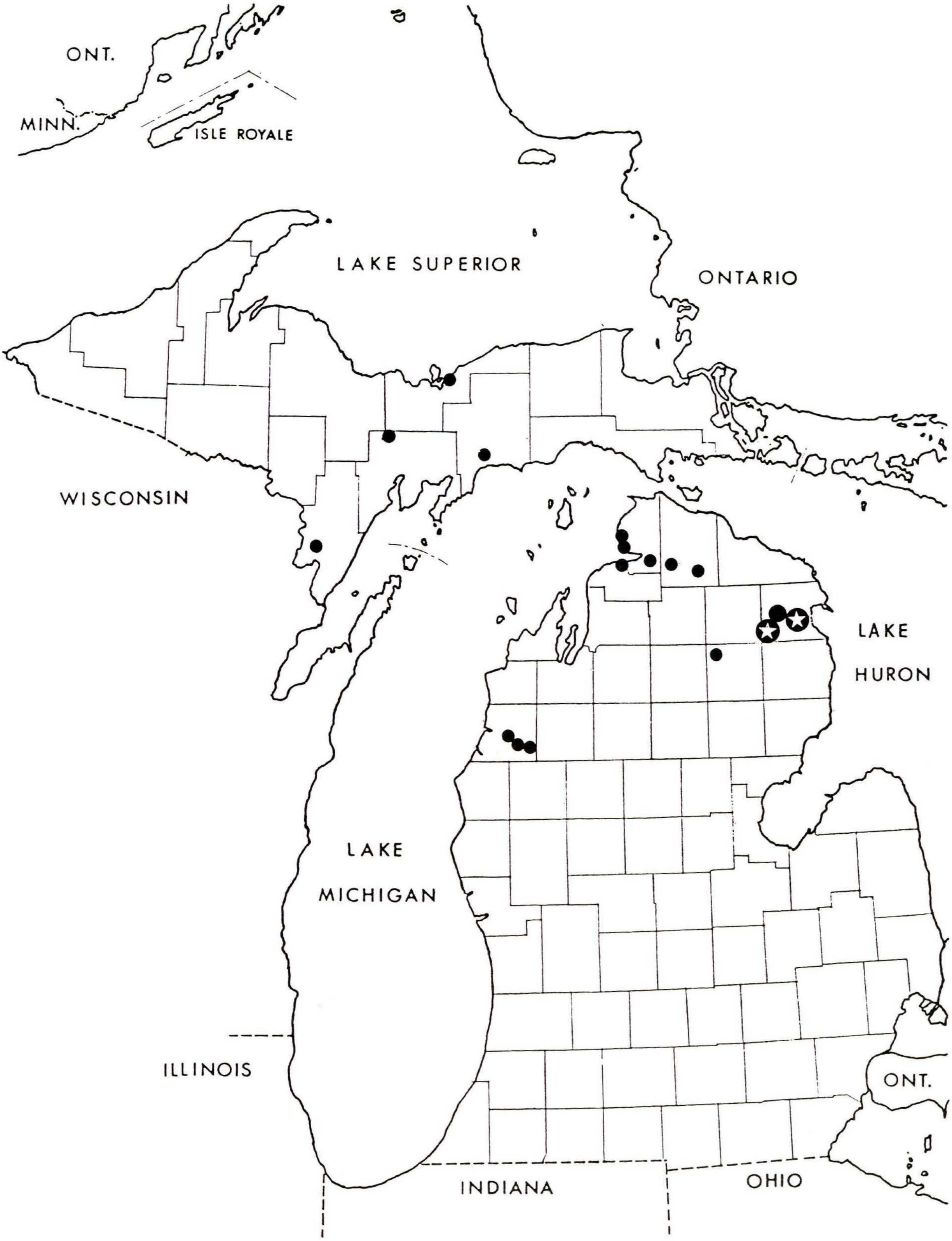
ONT.
MINN.
ISLE ROYALE
LAKE SUPERIOR
ONTARIO
WISCONSIN
LAKE HURON
LAKE MICHIGAN
ILLINOIS
ONT.
INDIANA
OHIO

Figure 1.—*Map of Michigan showing the locations of Barred Owl* (Strix varia) *study areas and of single breeding territories included in this study.* ✪ *= study area (see text);* ● *= one breeding territory;* ● *= three breeding territories.*

west of Alpena along both sides of an 11 km stretch of the Lower South Branch Thunder Bay River (LSBTBR) and tributary streams. The riparian habitat was mature riverbottom forest (silver maple, elm, ash); away from the river the forest cover was a patchwork of swampy deciduous/conifer mix, aspen-birch, and oak and pine on higher ground. The larger, but less intensively searched westerly area was centered on two large sportsmen's clubs near Fletcher Pond on the Alpena-Montmorency county line; the forest cover there was mainly second-growth sugar maple-beech with some aspen-birch stands and conifer swamp edge. Nests found opportunistically outside of these two study areas were situated in mature hardwood or mixed forest stands; one open nest was in a pine stand.

METHODS

Nests—natural and boxes—were checked at least twice each breeding season, the first time during April or early May to determine breeding activity. Adult owls seen sitting low in shallow cavities or open nests were assumed to be breeding, as were adults which came out of a cavity or box when the tree trunk or box was tapped or scratched with a stick. We located several cavity nests when adults became agitated and hooted at us when we came close to the nest site. The second visit was undertaken about the third week of May to determine reproductive success, band the young, sketch, describe and measure the nest site (if a tree cavity), and identify or collect prey remains and pellets. If the young were still too small (<2.5-3 weeks) the site was visited later. Our techniques were inadequate for assessing nonbreeding territorial pairs and possibly missed a few early nest failures. Nonbreeding pairs are hard to separate from pairs which may have moved to new, yet undiscovered tree cavities.

Terminology related to reproduction follows that of Postupalsky (1974) with some modifications. A breeding attempt means that eggs were laid or incubation behavior by an adult was observed. A successful attempt or productive nest is one in which at least one young was raised to fledging or near fledging age. Because nonbreeding pairs were not included in this study, productivity here means young/breeding attempt rather than young/territorial pair.

Scheller installed the first nest box in February 1979 after a previously used natural cavity in a dead stub had deteriorated beyond use and the owls had made two unsuccessful breeding attempts in a Red-shouldered Hawk (*Buteo lineatus*) nest nearby. The owls accepted the box the very first year. He then placed several additional boxes in the area, however, it wasn't until 1985 that any of them were accepted by owls. Over the years he has installed 20 boxes for Barred Owls, 18 in the eastern study area west of Alpena and two near Lachine. In 1983 and 1985 we installed 10 boxes built by Papp: eight in the Fletcher Pond study area, one near Lachine and one in southeastern Cheboygan County. Most boxes were placed within recently occupied breeding territories, preferrably where owls had used open nests or deteriorating natural cavities. Several were placed near where owls were seen or heard or in what we judged to be suitable habitat. Papp's boxes measured 30.5 x 25.4 cm on the inside, were 61 cm deep and open on top. Scheller's boxes were approximately 29 x 29 x 60 cm inside and were partially roofed-over; the entrance hole was partly in the roof and partly in the top of one side wall, or on a corner formed by the roof, one side wall and the front wall. All boxes were attached to deciduous trees, 5-6 m above ground.

In 1983 we started sketching and measuring tree cavities and cavity trees and snags used by Barred Owls. These measurements included:

1. Diameter at breast height (d.b.h.) of cavity tree or snag (cm);
2. Tree or limb diameter at the cavity (cm);
3. Height above ground, measured to the lowest point of cavity entrance (m);
4. Cavity depth, measured from lowest point of cavity entrance to cavity floor (cm);
5. Mean inside diameter of cavity, obtained by averaging the widest and narrowest inside measurements taken as close to the floor as possible (cm);
6. Cavity floor area (cm^2).

RESULTS AND DISCUSSION

We recorded 117 breeding attempts and determined breeding success for 114. Of these, 88 (77 percent) occurred in our Alpena County study areas (fig. 1). We identified 10 pair territories in the eastern area along the LSBTBR, six near Fletcher Pond, and three sites near Lachine, between the two study areas. The remaining 26 breeding attempts occurred at 10 territories elsewhere in the northern Lower

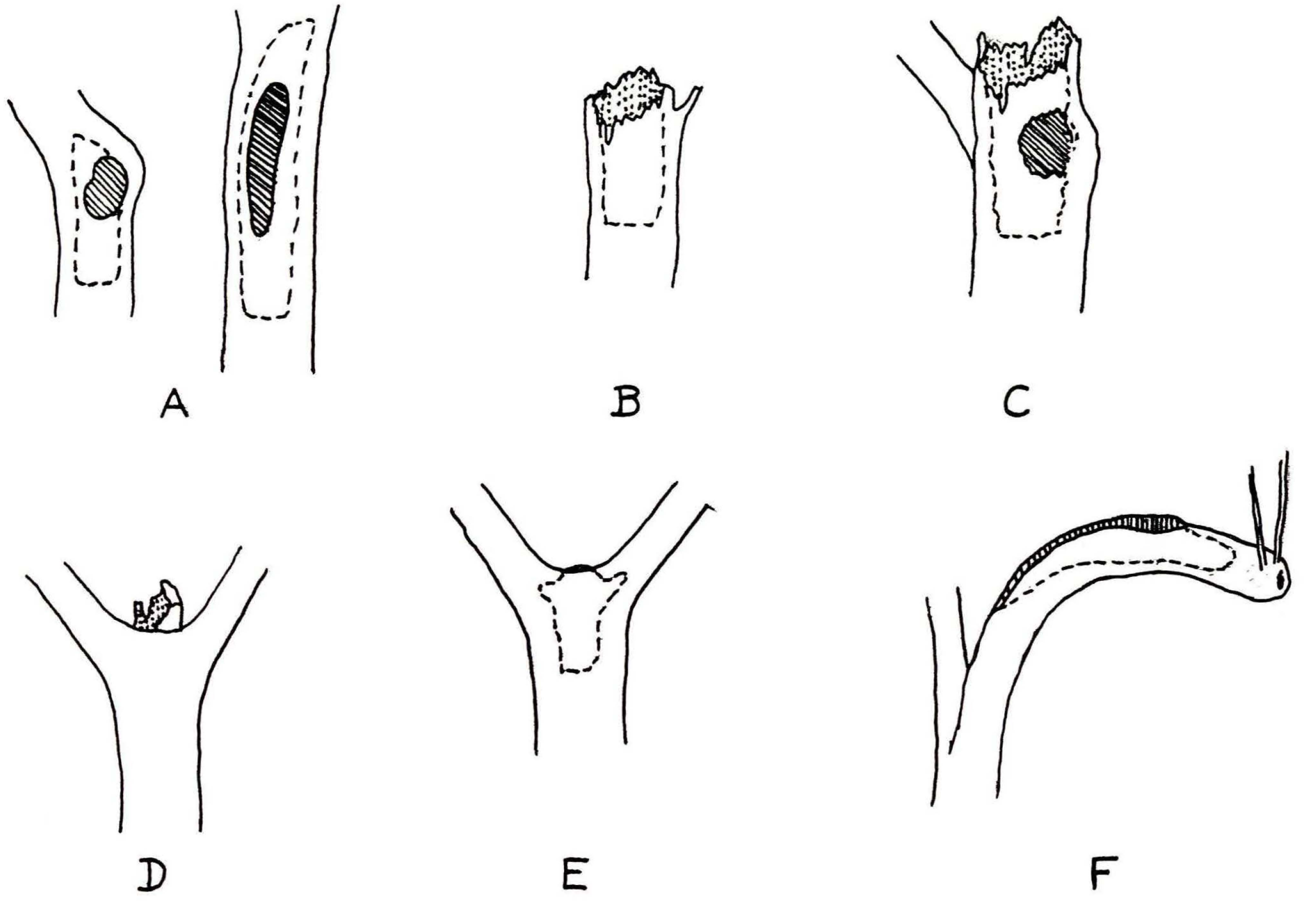

Figure 2.—*Barred Owl* (Strix varia) *nest sites: types of tree cavities and positions of entrance holes and numbers of each type encountered in northern Michigan.*

A.—Side entrance at site of broken-off limb 10
B.—Top entry (chimney) at top of stub or dead limb 7
C.—Chimney with second entry hole on side 3
D.—Tree fork with flat area partly enclosed by remainder of dead limb—no cavity 1
E.—Chimney in fork of live tree at site of broken-off limb or top 3
F.—Deformed live tree with cavity in slit within horizontal part 1

Peninsula, at four sites in the central Upper Peninsula of Michigan, and at one site in north-central Wisconsin (included to increase the sample size of open nests).

Nest Sites

Tree Cavities

Descriptions and Types of Cavities.—Owing to its size, the Barred Owl requires a spacious tree cavity with a large entrance hole for nesting; holes excavated by even the largest surviving North American woodpecker species, the Pileated Woodpecker (*Dryocopus pileatus*) are not large enough for Barred Owls. Most cavities used by Barred Owls can be assigned to one of two basic types: those within a hollow trunk with a side entrance and those with a more or less vertical "chimney" with a top entrance. The former (fig. 2 A) typically form by decay of the heartwood at the site of a broken-off limb. Depths of such cavities may range from a few centimeters below the lower rim of the entrance hole to more than 1 m. The entrance hole is usually more or less round or oval-shaped; in American beeches it often forms a slit, which can be up to 1.9 m long. Chimney-type cavities (fig. 2 B) occur in the tops of snags or large dead limbs, or in topped trees, often with live secondary tops. Chimney cavities ranged from the floor being nearly level

with the lowest portion of the wall to a depth of 92 cm. Deterioration of a snag or topped tree may eventually produce a chimney with both a top and side entrance (fig. 2 C).

Our observations suggest that a natural progression takes place as a dead tree top or vertical limb deteriorates. First, there may be a usable chimney cavity at the top. Then, as the limb gradually decays, only a low shell or partial shell remains, sheltering a flat area within the tree fork (fig. 2 D). As there was no cavity at one such nest site we found, we included it with the open nests. Finally, the remaining shell of the dead limb disappears completely and decay proceeds deeper into the trunk, forming a new chimney-type cavity with an opening in the tree fork (fig. 2 E). Such cavities are all but impossible to see from below.

The interior of snags and trunks of live trees may progressively decay upward from the roots, as well as downward from the top, eventually causing the cavity floor to collapse and thus render the hollow unusable for Barred Owls. In one instance we observed the owl using the upper cavity in the trunk of a beech tree, while an American porcupine (*Erethizon dorsatum*) was resting in the top of the lower hollow, no more than 30-50 cm below where the owl was incubating. On a later visit the porcupine was gone and one owlet was raised.

The strangest tree cavity we found was in a deformed sugar maple, bent over in the form of an inverted letter "L" (fig. 2 F). The horizontal portion was approximately 1.8 m from the ground and contained a long slit forming a shallow trough, which gradually became deeper and the cavity extended for a short distance (ca. 20 cm) beyond the slit into the "head" of the stub. Barred Owls nested in this deformed tree once during our study, raising at least one fledgling.

The numbers of each cavity type encountered are indicated in figure 2.

Cavity Trees.—The types and species of trees containing cavities and their frequency of use by Barred Owls are shown in table 1. Most cavities occurred in American beech trees (35 percent), followed by dead stubs and maples. Together, these three types accounted for 85 percent of 26 cavity sites identified. When frequency of use is considered, American beech becomes even more important; it was used for 48 percent of 50 breeding attempts, followed by maples and dead stubs used in 20 percent of attempts each. These three types together account for 88 percent of breeding attempts recorded in this study. The popularity of American beech may be related to the properties of its wood, which is heavy, rather hard, but not very durable when exposed to the elements (Otis 1931). Therefore cavities form

Table 1.—*Barred Owl* (Strix varia) *nest sites: species of cavity trees and frequency of their use in northern Michigan.*

	Individual trees		Frequency of use	
Tree species	**N**	**Percent**	**N**	**Percent**
American beech (*Fagus grandifolia* Ehrh.)	9	35	24	48
Sugar maple (*Acer saccharum* Marsh)	4	23	8	20
Silver maple (*Acer saccharinum* L.)	1		1	
Red maple (*Acer rubrum* L.)	1		1	
Yellow birch (*Betula alleghaniensis* Britton)	2	8	2	4
Red oak (*Quercus rubra* L.)	1	4	2	4
Quaking aspen (*Populus tremuloides* Michx.)	1	4	2	4
Dead stub	7	27	10	20
Aspen (*Populus* sp.)	(2)		(5)	
Elm (*Ulmus* sp.)	(1)		(1)	
Maple (*Acer* sp.)	(1)		(1)	
Unidentified deciduous tree	(2)		(2)	
Pine (*Pinus* sp.)	(1)		(1)	
Total	26	101	50	100

readily in beech trees and persist longer than in trees with softer wood.

Cavity Size.—Some measurements of nesting cavities are summarized in table 2 and compared to those obtained by Devereaux and Mosher (1984) in western Maryland, the only published Barred Owl cavity measurements we were able to find. Most of our Michigan nest measurement means and low values were somewhat lower than the corresponding data from the Maryland study. This may be due partly to the Maryland trees being generally larger and possibly to our larger sample size.

A d.b.h. of 48 cm should be viewed as the minimum tree size required by Barred Owls. In several trees the trunk diameter at the cavity was slightly larger than at breast height. In the tree with the lowest d.b.h. (27 cm) the cavity was situated within a nearly horizontal bend, and thus its size was larger than the cross-section of the trunk at breast height. As some cavities occur within large limbs, the diameter of such individual limbs is more relevant and the d.b.h. of the main trunk is correspondingly larger.

The lowest cavity was only 1.5 m above ground in the top of a burned-out pine stub; the breeding attempt failed.

Cavity size, as expressed by mean cavity diameter or by floor area, may be important in nest site selection by Barred Owls and may influence reproductive success. We observed that in small cavities the incubating adult appears quite cramped, often with its tail protruding out of the cavity opening or held upright along the inside wall. The relationship between cavity size and the owl's requirements for successful breeding, including adequate space for effective incubation and brooding, storage of prey items, and growth and development of young, needs to be investigated, as does the question whether cavity size affects clutch size and brood size.

Open Nests

Hawk Nests.—We recorded 10 Barred Owl breeding attempts in old hawk nests. Seven occurred in nests of the Red-shouldered Hawk, one in the nest of an unknown species, most likely a Red-shouldered or Broad-winged Hawk (*Buteo platypterus*), and two breeding attempts took place in successive years in the same Northern Goshawk (*Accipiter gentilis*) nest.

Other Open Nests.—We have observations of three breeding attempts in other types of open situations. One was a flat area in the fork of a yellow birch partly enclosed by the shell and overhang formed by the remnant of the third limb (described earlier), one was a ground nest, and the third was a man-made nest platform intended for Great Horned Owls.

Reproductive Success

Annual Monitoring.—During the two decades of this study we monitored between one and 16 Barred Owl breeding attempts each year. Initially (1976-1982) we followed between one and three nests, in 1983-1984 five, and in 1985-1990 between nine and 16. After 1990, due to other work commitments, Barred Owl monitoring was limited largely to Alpena

Table 2.—*Barred Owl* (Strix varia) *nest sites: means and ranges of cavity and cavity tree measurements in northern Michigan and western Maryland.*

	Northern Michigan[1]			Western Maryland[2]		
Measurement	**N**	**Mean**	**Range**	**N**	**Mean**	**Range**
D.b.h. (cm)	18	48.4	27-74	7	61	42-88
Tree diameter at cavity (cm)	14	44.5	30-64	4	46	36-54
Cavity height above ground (m)	22	6.8	1.5-12.8	7	9.1	4-14
Cavity depth (cm)	18	35.2	0-112	6	54	3-130
Mean inside diameter (cm)	19	25	18-44	6	33	22-41
Floor area (cm^2)	19	508	250-1,540	Not measured		

[1] This study.

[2] Devereaux and Mosher 1984.

County; we followed between three and six nests annually during 1991-1995.

The 1996 Season.—For the first time in 20 years we found no breeding Barred Owls in 1996—neither in natural sites nor in boxes. This was very likely a consequence of the hard 1995-1996 winter followed by a cool, late spring. After a brief thaw and rainy period about mid-February, temperatures dropped below freezing again, causing an ice crust to form on top of an already deep snow cover. This occurred along a wide area from Minnesota through northern Wisconsin into northern Michigan. A rash of reports followed of northern owls (mainly Boreal Owls, *Aegolius funereus*) as well as resident Barred Owls being found dead or in emaciated condition. Marge Gibson, a wildlife rehabilitator near Antigo, Wisconsin, received no fewer than 54 Barred Owls from various places in north-central Wisconsin during a 4.5 week period in February and March. All were thin and starving. Most had been picked up near human habitations—on roofs, in barns, near bird feeders, apparently attracted by small birds and rodents. Some were observed hunting during the day; and several were injured (and others killed) on roads while feeding on small road-kills (e.g., rabbits)—all indications of unusual behavior. In more "normal" winters Mrs. Gibson received one or two Barred Owls and no more than five during an entire year (M. Gibson, pers. comm.). Reports of dead and starving owls, including Barred, were also received from the Upper Peninsula and the northern Lower Peninsula of Michigan. Many more likely perished in the woods, undiscovered and unreported. There can be little doubt that over-winter mortality of Barred Owls was high and that evidently few of the surviving individuals were in good enough condition to breed in the late spring of 1996. In 1997 Barred Owls were again breeding in five of Scheller's nest boxes. All five breeding attempts were successful and 10 owlets (3, 3, 2, 1, 1) were produced. No breeding pairs were found in the western study area.

Reproductive Success.—Of 114 breeding attempts, 85 (75 percent) were successful in producing at least one young to fledging or to an advanced stage of development, i.e., banding age at 3-4.5 weeks (table 3). The exact brood size was unknown for 10 productive nests which were checked after the young owls had left the nest site and we were uncertain that we had found the entire brood. Such nests were considered in calculations of percent breeding success (see item B in tables 3-5), but were excluded from calculations of mean brood size. The mean brood size was 1.97 young/productive nest and the breeding productivity was 1.48 young/breeding attempt. The latter value is likely biased high, as we may have missed a small number of early-failing breeding attempts.

Although published data on Barred Owl reproductive success are few and rest on small sample sizes, they can offer some indications. Dunstan and Sample (1972) reported six breeding attempts in 6 years in the same tree

Table 3.—*Reproductive success of Barred Owls* (Strix varia) *in northern Michigan, 1976-1995.*

	Michigan[1]	**Minnesota**[2]
Breeding attempts [A]	114	22
Productive nests (all) [B]	85 (75%)	19 (86%)
Productive nests (known brood size) [C]	75	19
Nests with 1 young	18 (24%)	1 (5%)
Nests with 2 young	43 (57%)	10 (53%)
Nests with 3 young	12 (16%)	7 (37%)
Nests with 4 young	2 (3%)	1 (5%)
Total young (nests with known brood size) [D]	148	46
Young/productive nest (known brood size) [D/C]	1.97	2.42
Young/breeding attempt [D/C x B/A]	1.48	2.09

[1] This study (49 natural cavities, 52 nest boxes, 13 open nests).

[2] Johnson 1987 (1981-1986, all in nest boxes).

cavity in Minnesota. All six attempts were successful and 10 fledglings were raised, or 1.7 young/productive nest which in this case equals young/breeding attempt. Devereaux and Mosher (1984) studied eight nests in a 2-year study in western Maryland. One failed during the egg stage and seven contained 13 young; however, the outcome was determined for only five nests, of which only two (40 percent) were productive with a total of five fledglings. Mean brood size was 2.5 young/productive nest and productivity of 1.0 young/breeding attempt. Johnson (1987) reported 22 breeding attempts in nest boxes over a 6-year period in Minnesota. Nineteen (86 percent) were productive with mean brood size of 2.42 young/productive nest and productivity of 2.09 young/breeding attempt (table 3). All three measures of reproductive success in our study were lower than those in Johnson's (1987) work; this held also when breeding attempts in our nest boxes alone were compared (table 4). Apfelbaum and Seelbach (1983), using the North American Nest Record Card Program of Cornell University, calculated a mean brood size of 2.0 (N = 20) for Barred Owls in the Midwest and 2.02 (N = 55) in North America; these values are similar to our findings in this study.

More studies of reproductive success in different parts of the Barred Owl's breeding range are needed. Like Johnson (1987), we too have noted individual owls and pairs on their territories during the nonbreeding years. In the closely related Eurasian Ural Owl (*Strix uralensis*) and Tawny Owl (*S. aluco*) which, like the Barred Owl are resident, sedentary, and territorial, large proportions of the resident pairs do not breed (i.e., lay eggs) in low-prey years (Saurola 1989, Southern 1970). Therefore future research into Barred Owl breeding and population dynamics needs to include annual assessments of nonbreeding resident pairs.

Cavities versus Nest Boxes.—We recorded 50 breeding attempts in 26 different tree cavities and determined the success for 49 attempts. Of Scheller's 20 boxes near Alpena, 15 were used by owls for at least one breeding season. Of Papp's nine boxes near Fletcher Pond two were used a total of three times; his tenth box, in southeastern Cheboygan County, was used but once. In all, we monitored 54 breeding attempts in boxes and determined breeding success for 52 attempts.

Comparing reproductive success of Barred Owls in natural cavities to that in nest boxes (table 4), we saw a tendency toward larger broods in boxes. For the Tengmalm's Owl, the European subspecies of the Boreal Owl, Korpimäki (1984) found significantly larger clutches in boxes than in natural cavities; percent of eggs hatching and number of fledglings was also higher, but not significantly so. In another study Korpimäki (1985) reported that clutch size and breeding success in Tengmalm's Owls were related to box size. We do not have direct data on clutch size in Barred Owls, as we did not inspect the contents of nests during incubation. However, breeding success, the percent of breeding attempts producing at least one young, appeared lower in boxes than in natural cavities. The bottom line—productivity—was the same for both groups at 1.6 young/breeding attempt. The floor area in our boxes was larger than that measured in natural cavities ($\overline{x}$ = 508 cm^2, range: 259 - 1,540 cm^2, N = 19; table 2). Scheller's boxes had a floor area of approximately 850 cm^2 and Papp's of 775 cm^2. The relationship, if any, of floor area in cavities and boxes to brood size and other measures of reproductive success in Barred Owls requires further, more rigorous study.

Cavities and Boxes versus Open Nests.—Only one attempt of 10 in open hawk nests was successful and a single owlet was raised to banding age (ca. 3.5 weeks). Four hawk nests where adult owls were observed incubating early in the season were empty and deserted later, when large young should have been present. We found broken eggshells below one nest and a dead small owlet beneath each of two others. One nest which contained one small owlet earlier (seen from an adjacent tree) was empty and deserted on a follow-up visit. In yet another instance we found the nest empty and a 3-week-old owlet on the ground. The owlet was infested with "ear maggots" (*Protocalliphora*) and clusters of fly eggs adhering to feathers on its back. We took it to a rehabilitator for treatment and fostered it to a box 1 week later. As this owlet was unlikely to survive without our intervention, we counted this breeding attempt as unsuccessful.

There were three successful breeding attempts in other open situations. At least one young was raised in the open fork nest, one young fledged from the ground nest (details to be published elsewhere), and one owlet was

Table 4.—*Reproductive success of Barred Owls* (Strix varia) *in tree cavities and nest boxes in northern Michigan.*

	Tree cavities	Nest boxes
Breeding attempts [A]	49	52
Productive nests (all) [B]	42 (86%)	39 (75%)
Productive nests (known brood size) [C]	36	36
Nests with 1 young	9 (25%)	6 (17%)
Nests with 2 young	23 (64%)	20 (56%)
Nests with 3 young	3 (8%)	9 (25%)
Nests with 4 young	1 (3%)	1 (3%)
Total young (nests with known brood size) [D]	68	77
Young/productive nest (known brood size) [D/C]	1.89	2.14
Young/breeding attempt [D/C x B/A]	1.62	1.60

produced in the man-made nest platform. This platform, located in the Mead Wildlife Area in Marathon County, Wisconsin, was one of several Papp had placed in the Stevens Point area for Great Horned Owls. It consisted of an old 33-cm (13-inch) tire with one sidewall cut off and a bottom fastened to the opposite sidewall; the resulting bowl was attached to a tree fork 12.8 m above ground and partly filled with wood shavings. On 20 April 1985 Papp found two eggs, one of them pipped, and on 17 May he banded one owlet, at most 27 days old.

In table 5, Barred Owl reproductive success in enclosed sites—tree cavities and boxes—is compared to that in open nests. Few (31 percent) breeding attempts in open sites were successful and brood sizes at or near fledging age were small—1 young/productive nest. Such minimal brood sizes suggest that some owlets may have prematurely tumbled out of these nests as well; this appears likely in the only partially walled-in site in the tree fork and in the only successful breeding attempt in an old hawk nest. At 0.3 young/breeding attempt, productivity in open nests was less than one-fifth of that observed in cavities and boxes. For old hawk nests alone, productivity was only 0.1 young/breeding attempt, or one sixteenth that in enclosed sites.

In their unpublished study in northwestern Connecticut (1977-1982) Peter DeSimone and Michael Root found Barred Owls making four breeding attempts in open hawk and squirrel nests; all four failed. In contrast, 35 (81 percent) of 43 tree cavity nests were productive (P. DeSimone, pers. comm.).

Table 5.—*Reproductive success of Barred Owls* (Strix varia) *in northern Michigan: tree cavities and nest boxes compared to hawk nests and other open sites.*[1]

	Tree cavities & nest boxes	Open nests
Breeding attempts [A]	101	13
Productive nests (all) [B]	81 (80%)	4 (31%)
Productive nests (known brood size) [C]	72	3
Nests with 1 young	15 (21%)	3 (100%)
Nests with 2 young	43 (60%)	0
Nests with 3 young	12 (17%)	0
Nests with 4 young	2 (3%)	0
Total young (nests with known brood size) [D]	145	3
Young/productive nest (known brood size) [D/C]	2.01	1.0
Young/breeding attempt [D/C x B/A]	1.61	0.3

[1] One open nest in north-central Wisconsin included.

Causes of Poor Success in Open Nests

We conclude that the low success of Barred Owls using open nests is largely due to owlets falling out prematurely, before they are capable of climbing to safety, and either perish on the ground, or are killed outright by the fall. Note that two of the productive open nests did offer some degree of protection by at least partially "fencing" the young: at the flat site in the tree fork the remains of the dead limb served this purpose. Likewise, after the wood shavings had settled down in the tire platform, the owlet there was surrounded by a 8-10 cm high wall. In the ground nest the owlet had nowhere to fall and was brooded and cared for by the adult owl.

Other observers have also noted owlets falling from open nests. Bent (1938) found 38 Barred Owl nests in Massachusetts between 1891 and 1935. Of these, 18 were in old Red-shouldered Hawk and Cooper's Hawk (*Accipiter cooperii*) nests, five in what appeared to be old squirrel nests, and 15 in hollow trees. He provides no information on success in these different nest types, but comments (page 187) that "the increasing activities of the young reduce what was once a well-built and deeply hollowed nest to a smaller and flatter platform; this makes the nest increasingly dangerous as a cradle for the young...". Bent (1938) also reports finding "at least three young, half-grown or less, that have fallen from nests" and notes that he has never seen 4-5 week old owlets on the ground. We suggest that younger owlets would have been soon consumed by ground predators or scavengers, while older young would have climbed suitable trees and thus escaped notice.

In their monograph on the closely related Spotted Owl (*Strix occidentalis*) Forsman *et al.* (1984) write (page 36):

> "Nine owlets that were raised in platform nests fell or jumped from the nest when they were 15-25 days old. Of these, 7 were killed by the fall or disappeared before reaching the flying stage. No owlets were lost in this manner from cavity nests, suggesting that cavity nests provided a more secure environment for the young."

Forsman *et al.* (1984) state that normally young Spotted Owls leave the nest when 34-36 days old. Their "platforms" are what we call open nests, that is platforms of sticks or debris on limbs; about one-half (nine out of 17) were in old nests of hawks, squirrels, and woodrats. It then appears that loss of young from open nests is a problem in both owl species.

We propose that Barred Owls are obligate cavity nesters. Historically, there was no selective advantage in the acquisition of the necessary behavior patterns in their developing young to make them stay put in open nests, as young Great Gray (*Strix nebulosa*) and Great Horned Owls manage to do. While many Barred Owl fledglings may end up on the ground after leaving the nest, they are capable of climbing a tree by the time they reach fledging age (Dunstan and Sample 1972). From field tests with a small number of Barred Owl young we tentatively conclude that 3-week-old and younger owlets cannot effectively climb yet and that 4-week-old and older owlets can. Thus, if an owlet tumbles out of an open nest before attaining climbing proficiency, its survival prospects are very low. Obviously, trees with rough bark, such as white pine (*Pinus strobus* L.) are easier for young owls to negotiate than are trees with smooth, hard bark, such as beech.

Barred Owl breeding attempts in open nests, mainly those built by hawks, crows, and squirrels, may be an indication of a shortage of natural cavities resulting from past or current forestry practices and/or from increased competition for existing cavities with raccoons (*Procyon lotor*), opossums (*Didelphis virginiana*), squirrels (*Sciurus, Tamiasciurus*), and other tree-climbing mammals.

MANAGEMENT IMPLICATIONS

Statements that Barred Owls also use open nests are often repeated in the literature; however, until now, no information was available on the success of open nests. Most authors indicate or imply that use of open nests by this species is rare. Only Bent (1938) writes that 23 of the 38 nests of this owl he examined were open nests. We suggest, as has Yannielli (1991), that during the early part of this century Massachusetts second-growth forests may have been too young and lacked enough large trees with suitable cavities, which would have forced the owls to accept open nests. Nevertheless, reports such as Bent's (1938) have led some authors (and managers) to question the importance of cavities to Barred Owls. Yannielli (1991) expressed the view that "although cavities are preferred...they are not essential." This mistaken belief arises when investigators looking at habitat use and nest site selection pay little attention to reproductive success. Our findings confirm that use of open nests by Barred Owls is rare (11 percent in this study), and by showing that productivity in open nests is negligible, emphasize the critical importance of tree cavities to stable Barred Owl populations.

Forest managers should consider the great value of natural tree cavities in forest management plans. In selective cutting it is usually the dying, topped, diseased, deformed, "unsightly" trees which are removed. We often hear reports of loggers finding a cavity containing Barred Owl nestlings in a tree they had just cut down. Such incidents still occur on state as well as on private forests. The first step in managing for Barred Owls is the preservation of snags and an adequate number and dispersion of large live trees (> 50 cm d.b.h.) which contain, or are likely to develop suitable cavities. Dead stubs are subject to advanced decay, and are unlikely to persist for very long. Cavity trees, even those only partly alive are preferable.

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LITERATURE CITED

Apfelbaum, S.J.; Seelbach, P. 1983. Nest tree, habitat selection, and productivity of seven North American raptor species based on the Cornell University Nest Record Card Program. Raptor Research. 17: 97-113.

Bent, A.C. 1938. Life histories of North American birds of prey: part 2. U.S. Natl. Mus. Bull. 170. Washington DC. 482 p.

Bosakowski, T. 1994. Landsat reveals negative effect of forest fragmentation on Barred Owl distribution. Records of New Jersey Birds. 20: 66-70.

Bosakowski, T.; Speiser, R.; Benzinger, J. 1987. Distribution, density, and habitat relationships of the Barred Owl in northern New Jersey. In: Nero, R.W.; Clark, R.J.; Knapton, R.J.; Hamre, R.H., eds. Biology and conservation of northern forest owls; symposium proceedings; 1987 February 3-7; Winnipeg, Manitoba. Gen. Tech. Rep. RM-142. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 135-143.

Devereaux, J.G.; Mosher, J.A. 1984. Breeding ecology of Barred Owls in the central Appalachians. Raptor Research. 18: 49-58.

Dunbar, D.L.; Booth, B.P.; Forsman, E.D.; Hetherington, A.E.; Wilson, D.J. 1991. Status of Spotted Owl, *Strix occidentalis*, and Barred Owl, *Strix varia*, in southwestern British Columbia. Canadian Field-Naturalist. 105: 464-468.

Dunstan, T.C.; Sample, S.D. 1972. Biology of Barred Owls in Minnesota. Loon. 44: 111-115.

Elody, B.I.; Sloan, N.F. 1985. Movements and habitat use of Barred Owls in the Huron Mountains of Marquette County, Michigan, as determined by radiotelemetry. Warbler. 63: 3-8.

Errington, P.L. 1930. The pellet analysis method of raptor food habits study. Condor. 32: 293-296.

Errington, P.L. 1932a. Techniques of raptor food habits study. Condor. 34: 75-86.

Errington, P.L. 1932b. Food habits of southern Wisconsin raptors. Part I. Owls. Condor. 34: 176-186.

Errington, P.L.; McDonald, M. 1937. Conclusions as to the food habits of the Barred Owl in Iowa. Birdlife. 7: 47-49.

Forsman, E.D.; Meslow, E.C.; Wright, H.M. 1984. Distribution and biology of the Spotted Owl in Oregon. Wildlife Monographs. 87: 1-64.

Fuller, M.R. 1979. Spatiotemporal ecology of four sympatric raptor species. St. Paul, MN: University of Minnesota. 220 p. Ph.D. dissertation.

Hamer, T.E.; Forsman, E.D.; Fuchs, A.D.; Walters, M.L. 1994. Hybridization between Barred and Spotted Owls. Auk. 111: 478-492.

Hamerstrom, F.N., Jr.; Hamerstron, F. 1951. Food of young raptors on the Edwin S. George Reserve. Wilson Bulletin. 63: 16-25.

Johnson, D.H. 1987. Barred Owls and nest boxes—results of a five-year study in Minnesota. In: Nero, R.W.; Clark, R.J.; Knapton, R.J.; Hamre, R.H., eds. Biology and conservation of northern forest owls: symposium proceedings; 1987 February 3-7; Winnipeg, Manitoba. Gen. Tech. Rep. RM-142. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 129-134.

Korpimäki, E. 1984. Clutch size and breeding success of Tengmalm's Owl *Aegolius funereus* in natural cavities and nest-boxes. Ornis Fennica. 61: 80-83.

Korpimäki, E. 1985. Clutch size and breeding success in relation to nest-box size in Tengmalm's Owl *Aegolius funereus*. Holarctic Ecology. 8: 175-180.

Korschgen, L.J.; Stuart, H.B. 1972. Twenty years of avian predator-small mammal relationships in Missouri. Journal of Wildlife Management. 36: 269-282.

Laidig, K.J.; Dobkin, D.S. 1995. Spatial overlap and habitat associations of Barred Owls and Great Horned Owls in southern New Jersey. Journal of Raptor Research. 29: 151-157.

McGarigal, K.; Fraser, J.D. 1984. The effect of forest stand age on owl distribution in southwestern Virginia. Journal of Wildlife Management. 48: 1393-1398.

Mendall, H.L. 1944. Food hawks and owls in Maine. Journal of Wildlife Management. 8: 198-208.

Nicholls, T.H.; Fuller; M.R. 1987. Territorial aspects of Barred Owl home range and behavior in Minnesota. In: Nero, R.W.; Clark, R.J.; Knapton, R.J.; Hamre, R.H., eds. Biology and conservation of northern forest owls; symposium proceedings; 1987 February 3-7; Winnipeg, Manitoba; Gen. Tech. Rep. RM-142. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 121-128.

Nicholls, T.H.; Warner, D.W. 1972. Barred Owl habitat use as determined by radiotelemetry. Journal of Wildlife Management. 36: 213-224.

Otis, C.H. 1931. Michigan trees: a handbook of the native and most important introduced species. Ann Arbor, MI: University of Michigan Press. 362 p.

Postupalsky, S. 1974. Raptor reproductive success: some problems with methods, criteria and terminology. In: Hamerstrom, F.N.; Harrell, B.E.; Olendorff, R.R., eds. Management of raptors: proceedings of the conference on raptor conservation techniques; 1973 March 22-24; Fort Collins, CO. Raptor Res. Rep. Raptor Research Foundation. 2: 21-31. [part 4].

Saurola, P. 1989. Breeding strategy of the Ural Owl *Strix uralensis*. In: Meyburg, B.-U.; Chancellor, R.D., eds. Raptors in the modern world: proceedings of the 3d world conference on birds of prey and owls; 1987 March 22-27; Eilat, Israel. Berlin, London, Paris: World Working Group on Birds of Prey and Owls: 335-340.

Southern, H.N. 1970. The natural control of a population of Tawny Owls (*Strix aluco*). Journal of Zoological Society London. 162: 197-285.

Taylor, A.L.; Forsman, E.D. 1976. Recent range expansion of the Barred Owl in western North America, including the first records for Oregon. Condor. 78: 560-561.

Wilson, K.A. 1938. Owl studies at Ann Arbor, Michigan. Auk. 55: 187-197.

Yannielli, L.C. 1991. Preferred habitat of northern Barred Owls in Litchfield County, Connecticut. Connecticut Warbler. 11: 12-20.

Effectiveness of Broadcast Surveys in Determining Habitat Use of Ferruginous Pygmy-owls (*Glaucidium brasilianum*) in Southern Texas

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Abstract.—We compared habitat information obtained from tracking 12 radio-tagged Ferruginous Pygmy-owls (*Glaucidium brasilianum*) (hereafter referred to as pygmy-owls) in southern Texas during 1995 and similar information from pygmy-owl response points to evaluate the effectiveness of broadcast surveys in determining pygmy-owl habitat use. Response points were established beneath pygmy-owls that responded to broadcasted conspecific calls. Broadcast stations (n = 303) were established throughout the study area following systematic-random protocol. To obtain habitat information, a 0.04 ha circular plot was established at pygmy-owl response points (n = 37) and on > 24 hour intervals at visual sighting points of radio-tagged pygmy owls (n = 292). Using systematic-random sampling, 217 0.04 ha circular plots were established throughout the study area to determine forest composition. Broadcast surveys were conducted from 22 January-31 June 1995. Radio-tagged pygmy-owls were tracked from 3 April-6 October 1995. We used two-tailed Z-tests to compare the mean number of trees in nine categories, based on the trees' diameter at breast height (d.b.h.), and to compare understory values obtained at the four cardinal directions of each plot. Results from 8 d.b.h. categories showed no significant difference (P = > 0.05) in habitat composition of areas used by radio-tagged pygmy-owls and areas beneath pygmy-owls responding to broadcast calls. In addition, no significant difference (P = > 0.05) in mean understory values of areas used by radio-tagged pygmy-owls and pygmy-owl response points was recorded. However, 5 d.b.h. categories showed a significant difference (P = > 0.05) between habitat composition of areas used by radio-tagged pygmy-owls and the overall study area. Understory values of areas used by radio-tagged pygmy-owls were significantly different (P = < 0.05) from their availability on the study area. Therefore, results indicate pygmy-owls were not using habitat in direct proportion to its availability, and broadcast surveys may be a viable means of determining habitat use of Ferruginous Pygmy-owls in southern Texas.

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Comparison of Food Habits of the Northern Saw-whet Owl (*Aegolius acadicus*) and the Western Screech-owl (*Otus kennicottii*) in Southwestern Idaho

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Abstract.—I compared the breeding-season diets of Northern Saw-whet Owls (*Aegolius acadicus*) and Western Screech-owls (*Otus kennicottii*). Prey items were obtained from regurgitated pellets collected from saw-whet owl and screech-owl nests found in nest boxes in the Snake River Birds of Prey National Conservation Area in southwestern Idaho. A total of 2,250 prey items of saw-whet owls and 702 prey items of screech-owls were identified. Saw-whet owl diet was analyzed for the years 1990-1993; screech-owl diet was analyzed for 1992 only. The most frequently found prey items in the saw-whet owls diet were: *Peromyscus, Mus, Microtus and Reithrodontomys;* there were no significant differences among years. When saw-whet owl prey frequency data were pooled across years and compared to the 1992 screech-owl data, significant differences in diet were found. However, a comparison of the 1992 saw-whet prey frequency data with the screech-owl data showed no significant differences. In addition, the among year saw-whet owl prey biomass was analyzed, and again there were no significant differences. *Microtus,* followed by *Mus,* accounted for the largest proportion of prey biomass (by percent) in the diets of saw-whet owls for all years. When saw-whet owl prey biomass data were pooled across years and compared to the 1992 screech-owl prey biomass, significant differences in diet were found. The 1992 saw-whet prey biomass compared to the 1992 screech-owl prey biomass also was significantly different. Saw-whet owl prey biomass fell mainly between 11 and 55 grams; screech-owl prey biomass was more evenly distributed across the weight classes (0.5 grams - 400 grams).

Northern Saw-whet Owls (*Aegolius acadicus*) and Western Screech-owls (*Otus kennicottii*) inhabit many different habitat types and are sympatric in many areas of their ranges (Johnsgard 1988). Saw-whet owl diet varies with habitat type (Cannings 1987, Dinsmore and Clark 1991, Holt and Leroux 1996, Swengel and Swengel 1992, Marks and Doremus 1988), and though few data are available for the Western Screech-owl it is reasonable to expect that screech-owl diet also will vary with habitat type. The Western Screech-owl has a varied diet, including small mammals, birds, and invertebrates (Barrows 1989, Brown *et al.* 1987, Marks and Marks 1981, Smith and Wilson 1971), and appears to be broader than that of the saw-whet owl whose diet tends to concentrate on a few small mammals (Cannings 1987, Dinsmore and Clark 1991, Holt and Leroux 1996, Swengel and Swengel 1992, Marks and Doremus 1988). I collected and analyzed breeding season pellets in order to characterize and compare Saw-whet Owl and Western Screech-owl diets in southwestern Idaho.

METHODS

Study Area

This study was conducted in southwestern Idaho in the Snake River Birds of Prey National Conservation Area (NCA) and the adjacent C.J. Strike Wildlife Management Area (WMA); these were administered by the Bureau of Land

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Management (BLM), and Idaho Department Fish and Game, respectively. Habitat in both areas was composed of a slightly-rolling shrub-steppe desert cut by the canyons of the Snake and Bruneau rivers. Vegetation within the riparian habitats consists of scattered groves of Russian olive (*Eleaegnus angustifolia)*, black locust (*Robinia pseudocacia*), and willow (*Salix* spp.). Vegetation outside of the riparian areas was dominated by big sagebrush (*Artemisia tridentata*) associations, and introduced cheatgrass (*Bromus tectorium*). Public lands in the study area were interspersed with irrigated private cropland; elevation ranged from 775-1,000 m. USDI (1979) provides a more complete description of the vegetation and topography of the area.

In 1982, BLM began placing nest boxes in the riparian areas of the NCA and WMA for Western Screech-owls. Since then, more than 94 boxes have been placed in the study area. The first recorded nesting of Northern Saw-whet Owls within the study area occurred in 1986.

Food Habits

During my monitoring of the nesting saw-whet owls, whenever possible cached prey items were removed from the nest boxes and identified. The prey items were identified using field guides, and recorded. If the prey items were intact, the head and legs were removed to avoid the possibility of recounting the prey items in a pellet. No cached prey items were identified from the nest boxes of screech-owls.

Saw-whet owl and screech-owl pellets were collected from nest boxes during and after the breeding season. I also collected all of the nesting material (wood chips) after each nesting attempt had been completed or terminated. Because of the large volume of this material, it was processed using a modification of the procedure described by Marti (1987). Feathers and insect parts were first removed from the nesting material. The remaining material was then soaked in a dilute (10 percent) NaOH solution for several hours to dissolve hair. Subsequently, any parts of prey remains that could be used for identification were separated from the wood chips. Identifiable prey remains included: skulls, mandibles, dentaries, pelvic bones, limb bones, beaks, avian feet, and insect and crustacean body parts. A dissecting microscope was used in identifying prey remains. To identify prey items, I compared the remains to museum specimens or a skull key (Glass 1981). Most mammalian prey was identified to genus; other prey was identified to class.

Prey items were enumerated by counting left and right fragments of both the upper and lower jaws. A total count was determined by tabulating the largest possible number derived from the four counts. Some fragments were too small or were missing key parts for proper identification. These prey items were listed as "unknown." The total number of unknown items was determined by subtracting the number of missing pieces of the known items from the unknown items. For example, if a prey item was missing a left lower jaw, then a left lower jaw was subtracted from the unknown left lower jaw total. This method assured that no items were counted as "unknown" when they were actually a missing fragment of one of the known prey items.

Biomass of mammalian and avian prey was estimated using average weights (Dunning 1993, Steenhof 1983). Because bird remains were not identified beyond class, species of birds known to be prey of saw-whet owls and screech-owls and that were known to be in the study area, were used to calculate the avian biomass estimates (Holt and Leroux 1996, Ritchison and Cavanagh 1992). Other screech-owl prey biomass estimates were obtained from prey use of Eastern Screech-owls in Kentucky (Ritchison and Cavanagh 1992).

Food habit differences for saw-whet owls and screech-owls were statistically analyzed using SAS for Personal Computers (SAS Institute Inc. 1985). MANOVA analyses were used to test whether prey frequency and percent biomass differed significantly among years and between owl species.

RESULTS

Food Habits

Prey Frequency

The diet of saw-whet owls was analyzed for the years 1990-1993; there was no significant difference in saw-whet diet composition among years. Table 1 shows the pooled frequency of numbers (c.f. Marti 1987) of all prey species in the diet of saw-whet owls. In all years, *Mus, Microtus, Peromyscus,* and *Reithrodontomys*

Table 1.—*Percent frequency and percent estimated biomass of 2,250 prey taken by Northern Saw-whet Owls (*Aegolius acadicus*) taken from 20 nest sites (nest boxes) within the Snake River Birds of Prey National Conservation Area, southwestern Idaho. The 1990-1993 data has been pooled as there were no significant differences among years.*

Prey species	**Frequency**	**Biomass**
	----- *Percent* -----	
Peromyscus	21.29	17.58
Mus	30.70	27.03
Microtus	25.16	43.46
Reithrodontomys	14.27	6.81
Sorex	2.58	0.60
Perognathus	0.37	0.35
Onychomys	0.29	0.29
Bird	1.03	0.84
Unknown	4.30	3.03

Table 2.—*Percent frequency and percent estimated biomass of 702 prey taken by Western Screech-owls (*Otus kennicottii*) from 11 nest sites (nest boxes) within the Snake River Birds of Prey National Conservation Area, southwestern Idaho. All prey items were from the 1992 nesting season.*

Prey species	**Frequency**	**Biomass**
	----- *Percent* -----	
Peromyscus	15.00	10.77
Mus	17.37	12.19
Microtus	12.86	23.66
Reithrodontomys	17.81	7.44
Sorex	0.66	0.16
Perognathus	13.18	8.20
Dipodomys	9.67	19.23
Thomomys	1.07	8.03
Spermophilus	0.12	0.86
Neotoma	0.12	1.41
Bird	2.23	2.67
Insect	0.99	0.02
Crayfish	0.40	0.09
Lizard	0.28	0.19
Fish	0.12	0.05
Unknown	8.11	5.04

comprised the largest proportions of prey items in the diet.

Table 2 shows the frequency of numbers of all prey species in the diet of screech-owls for the year 1992. *Reithrodontomys*, *Mus*, and *Peromyscus* comprised the largest proportions of prey items.

The pooled saw-whet owl diet data were compared to the 1992 diet data of screech-owls (fig. 1). Screech-owl diet data was only available for the year 1992. Note that screech-owls had a broader diet including: ground squirrels, fish, lizards, and crayfish that were not found in the saw-whet diet. There were totals of 2,250 saw-whet and 702 screech-owl prey items. There was a significant difference between the mean prey item frequency for the pooled saw-whet owl data and the screech-owl data, F = 3.83, df = 13, 16, p = 0.009. I also compared prey frequency for just the 1992 saw-whet owl data and the 1992 screech-owl data. There was no significant difference in prey frequency between saw-whet owl and screech-owls in 1992.

Prey Biomass

Table 1 also presents the estimated biomass that each prey type contributed to the saw-whet owl diet (years pooled). Analysis of among year saw-whet owl mean prey biomass did not reveal any significant differences. The largest proportion of prey biomass was *Microtus* followed by *Mus* and *Peromyscus*.

There was a significant difference (F = 3.63, df = 13, 16, p = 0.011) between the pooled saw-whet prey biomass data and the 1992 screech-owl prey biomass (fig. 2). The 1992 saw-whet prey biomass and the 1992 screech-owl prey biomass were also significantly different (F = 885.8, df = 1, 16, p = 0.026).

I then compared the biomass size class of prey taken by saw-whet owls with that taken by screech-owls (fig. 3). Here the 0.5-10 grams size class included *Sorex* and insects; the 11-20 grams—*Peromyscus* and *Mus*; the 31-50 grams—*Microtus*; the 51-100 grams—*Onychomys*, and the 101-400 grams—*Spermophilus*, *Neotoma*, and *Thomomys*. Figure 3 shows that screech-owl prey biomass is distributed across a broader range of size classes than that of the saw-whet owl.

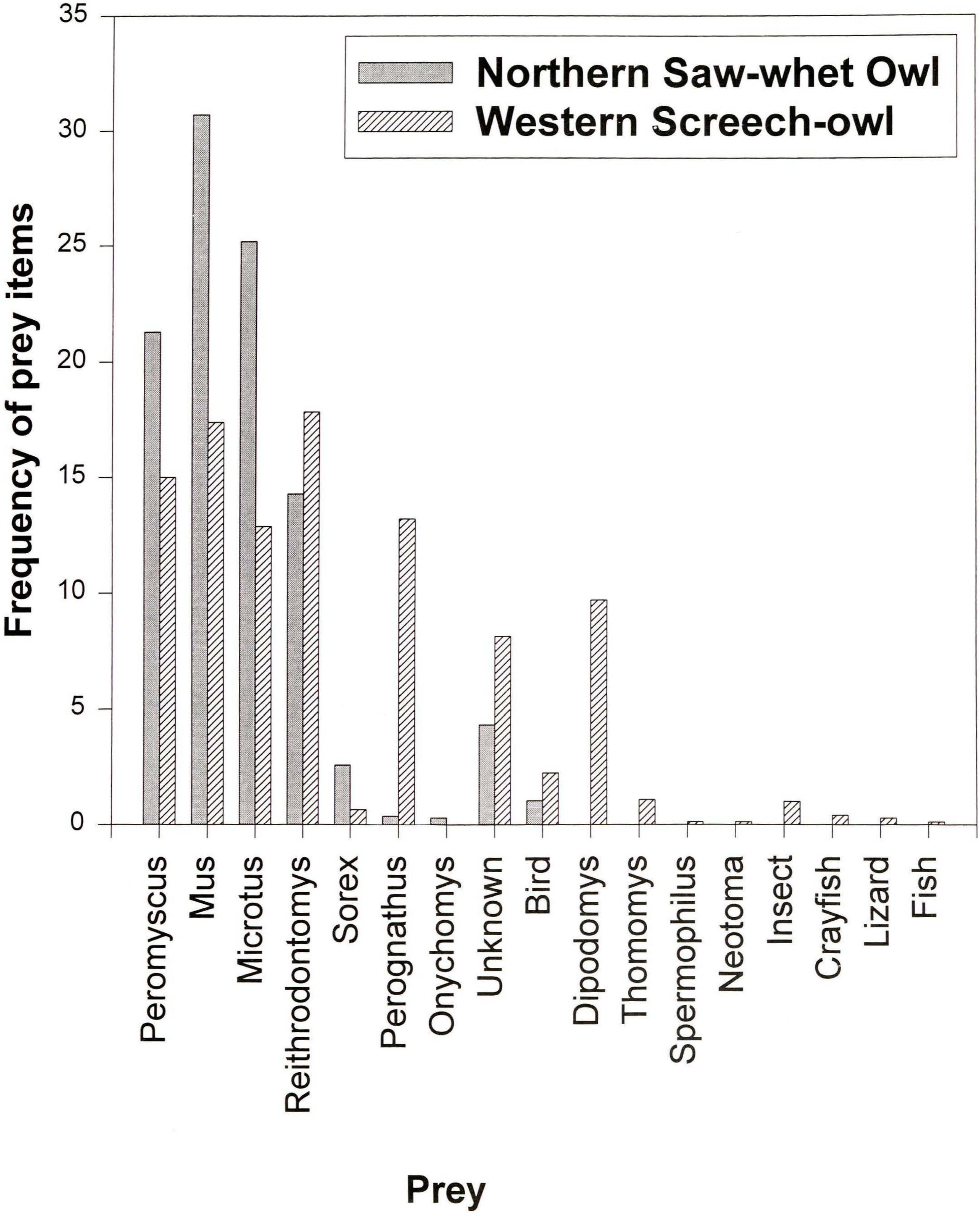

Figure 1.—*Comparison of the prey frequency during the breeding season of Northern Saw-whet Owls (*Aegolius acadicus*) (1990-1993) and Western Screech-owls (*Otus kennicottii*) (1992) within the Snake River Birds of Prey National Conservation Area, Southwestern Idaho. The MANOVA showed a significant difference between the two owl species (F = 3.83, df = 13, 16, p = 0.009).*

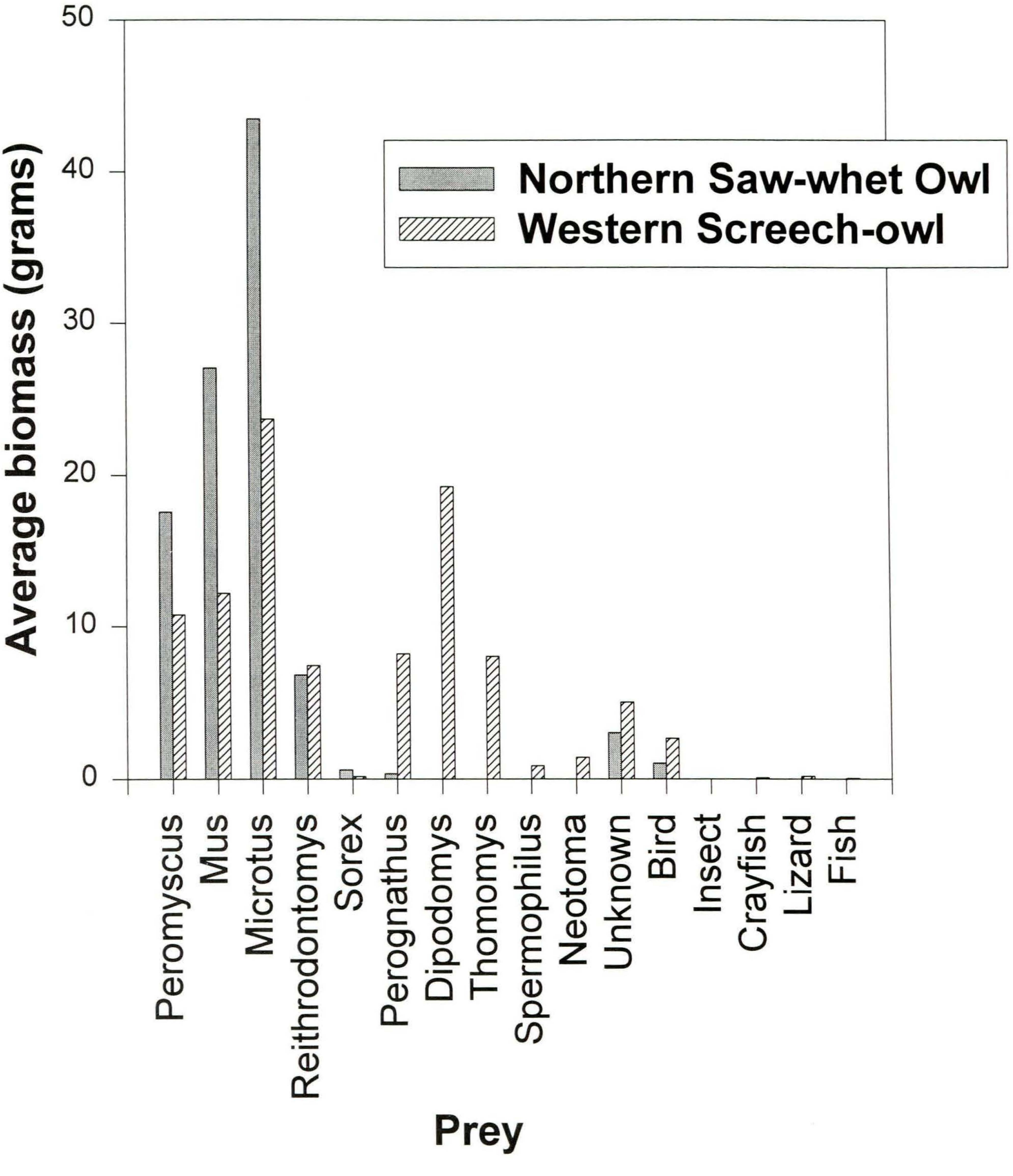

Figure 2.—*Comparison of the prey biomass (grams) of Northern Saw-whet Owls* (Aegolius acadicus) *and Western Screech-owls* (Otus kennicottii) *nesting within the Snake River Birds of Prey National Conservation Area, southwestern Idaho. The MANOVA showed a significant difference between the two owl species (F = 3.63, df = 13, 16, p = 0.011).*

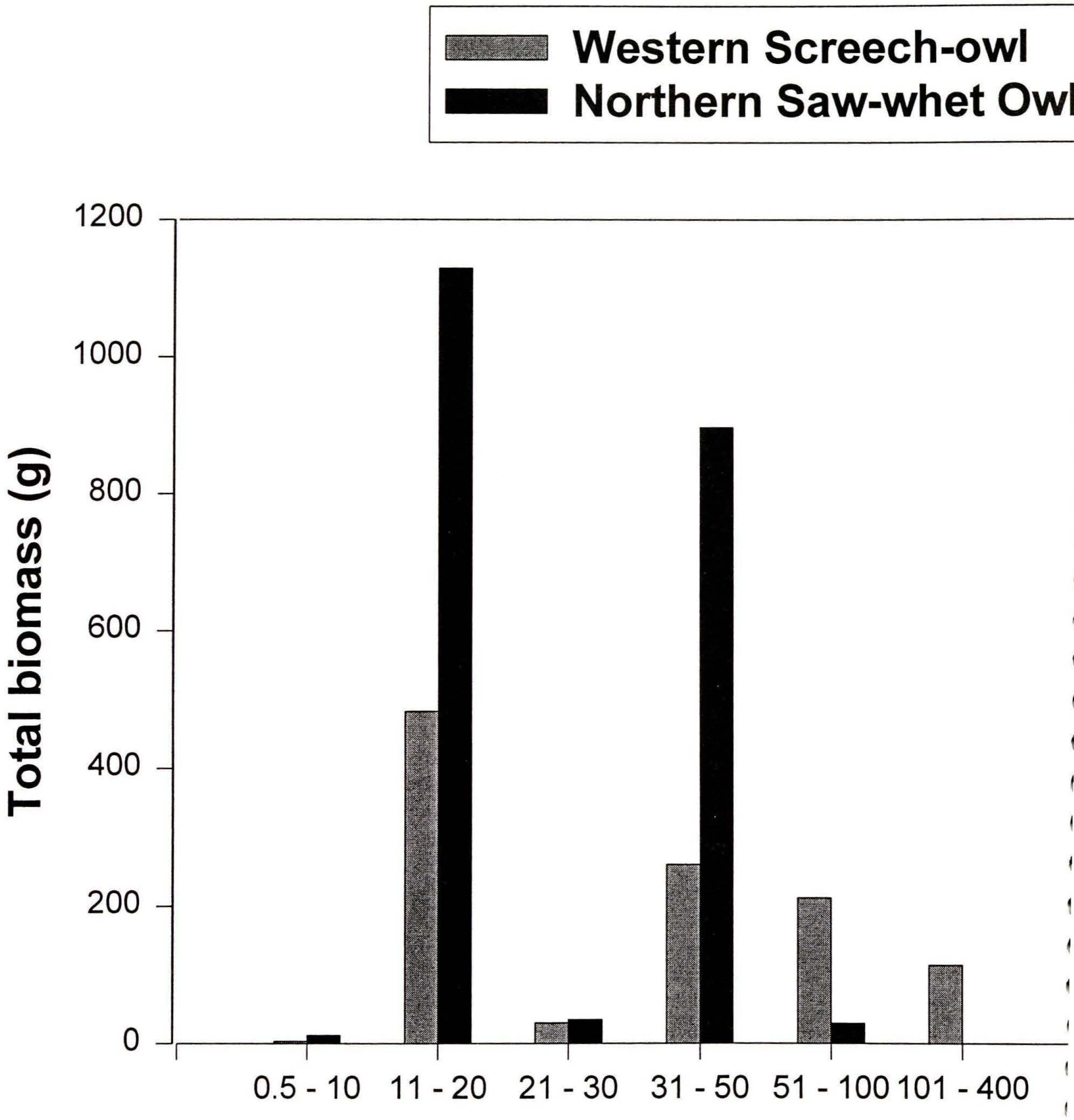

Figure 3.—*Comparison of the pooled prey biomass (grams) by weight of Northern Saw-whet Owls (*Aegolius acadicus*) and Western Screech-owls (*Otus kennicottii*) nesting within the Snake River Birds of Prey National Conservation Area, southwestern Idaho. The 0.5-10 gram class would include* Sorex *and insects, 11-20 grams:* Peromyscus *and* Mus, *31-50 grams:* Microtus, *51-100 grams:* Dipodomys, *and 101-400 grams:* Neotoma, Spermophilus, *and* Thomomys.

DISCUSSION

Food habits of Northern Saw-whet Owls have been reported for the non-breeding season (Dinsmore and Clark 1991, Holt *et al.* 1990, Swengel and Swengel 1992) and for the breeding-season (Cannings 1987, Holt and Leroux 1996, Marks and Doremus 1988). Here I have provided breeding-season diet data. My study results concurred with an earlier study in the Snake River Birds of Prey NCA which found *Mus* to be the most numerous prey (Marks and Doremus 1988); my results place *Mus, Microtus*, and *Peromyscus* as the three most numerous prey taken. However, Holt and Leroux (1996) noted that *Microtus* was the most frequently taken prey species in Montana. The non-breeding season studies noted that *Peromyscus* was the most frequently consumed prey item (Dinsmore and Clark 1991, Holt *et al.* 1990, Swengel and Swengel 1992). The results of my study were similar to Cannings (1987) who found that *Microtus* was the most important prey in biomass but not in frequency.

Relatively few studies have been done on the food habits of Western Screech-owls. In my study, *Reithrodontomys* was the prey most frequently consumed by screech-owls followed by *Mus, Peromyscus, Perognathus, Microtus, Dipodomys*, and birds. The most frequently identified prey item in other studies were *Passer domesticus* (Smith and Wilson 1971), *Dipodomys* (Brown *et al.* 1987), *Peromyscus* (Marks and Marks 1981), and *Perognathus* (Barrows 1989). I found *Microtus* and *Dipodomys* to be the most important prey in terms of biomass. Marks and Marks (1981) noted that *Peromyscus* composed 62 percent of screech-owl diet biomass, while *Passer domesticus* made up 50 percent of the diet biomass of wintering screech-owls in Utah (Smith and Wilson 1971).

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LITERATURE CITED

Barrows, C.W. 1989. Diets of five species of desert owls. Western Birds. 20(1): 1-10.

Brown, B.A.; Whitaker, J.O.; French, T.W.; Maser, C. 1987. Note on food habits of the screech owl and the Burrowing Owl of southeastern Oregon. Great Basin Naturalist. 46(3): 421-426.

Cannings, R.J. 1987. The breeding biology of Northern Saw-whet Owls in southern British Columbia. In: Nero, R.W.; Clark, R.J.; Knapton, R.J.; Hamre, R.H., eds. Biology and conservation of northern forest owls: symposium proceedings; 1987 February 3-7; Winnipeg, Manitoba. Gen. Tech. Rep. RM-142. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 193-198.

Dinsmore, S.J.; Clark, W.R. 1991. Food habits of the Northern Saw-whet Owl in central Iowa: effects of roost location. Joural of the Iowa Academy of Science. 98(4): 167-169.

Dunning, J.B., Jr., ed. 1993. CRC handbook of avian body masses. Boca Raton, FL: CRC Press, Inc. 371 p.

Glass, B.P. 1981. A key to the skulls of North American mammals. Stillwater, OK: Department of Zoology, Oklahoma State University. 59 p.

Holt, D.W.; Leroux, L.A. 1996. Diets of Northern Pygmy-owls and Northern Saw-whet Owls in west-central Montana. Wilson Bulletin. 108(1): 123-128.

Holt, D.W.; Andrews, E.; Claflin, N. 1990. Nonbreeding season diet of Northern Saw-whet Owls, *Aegolius acadicus*, on Nantucket Island, Massachusetts. Canadian Field-Naturalist. 105(3): 382-385.

Johnsgard, P.A. 1988. North American owls: biology and natural history. Washington, DC: Smithsonian Institution Press.

Marks, J.S.; Doremus, J.D. 1988. Breeding-season diet of Northern Saw-whet Owls in southwestern Idaho. Wilson Bulletin. 100(4): 690-694.

Marks, J.S.; Marks, V.A. 1981. Comparative food habits of the screech owl and Long-eared Owl in southwestern Idaho. Murrelet. 62: 80-82.

Marti, C.D. 1987. Raptor food habits studies. In: Pendleton, B.A.; Millsap, B.A.; Kline, K.W.; Bird, D.A., eds. Raptor management techniques manual. Washington, DC: National Wildlife Federation Scientific and Technical Series 10: 67-80.

Ritchison, G.; Cavanagh, P.M. 1992. Prey use by Eastern Screech-owls: seasonal variation in Central Kentucky and a review of previous studies. Journal of Raptor Research. 26(2): 66-73.

SAS Institute Inc. 1985. SAS® introductory guide for personal computers, Vs. 6 ed. Cary, NC: SAS Institute Inc. 111 p.

Smith, D.G.; Wilson, C.R. 1971. Notes on the winter food of screech owls in central Utah. Great Basin Naturalist. 31(2): 83-84.

Steenhof, K. 1983. Prey weights for computing percent biomass in raptor diets. Journal of Raptor Research. 17(1): 15-27.

Swengel, S.R.; Swengel, A.B. 1992. Diet of Northern Saw-whet Owls in southern Wisconsin. Condor. 94: 707-711.

U.S. Department of Interior. 1979. Snake River birds of prey special research report. Boise, ID: Bureau of Land Management, Boise District.

Non-territorial Floaters in Great Horned Owls *(Bubo virginianus)*

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Abstract.—The ecology and behavior of non-territorial owls are basically unknown. I studied the integration of young Great Horned Owls *(Bubo virginianus)* into the territorial breeding population from 1988-1993 in the southwestern Yukon, Canada, during a peak and decline of the population cycle of snowshoe hares *(Lepus americanus)*. Fifty-five fledglings were equipped with radio-transmitters that allowed weekly monitoring of individuals for 2-3 years. After a synchronized dispersal phase in each September, 29-45 percent remained within 35 km of their natal territories. Although 15 percent settled in a territory and were capable of reproducing before the end of their first year of life, most of these owls became non-territorial floaters. Several lines of evidence indicated that this behavior was caused by territorial exclusion of breeding pairs. Floaters were secretive and mostly resident within home ranges that were about five times the size of average territories. Movement patterns suggested that floaters were not involved in extra-pair matings, and that floating is not an alternative reproductive strategy. Survival of floaters was very high during peak densities of prey, leading to a proportion of 40-50 percent of non-territorial owls in the population. When numbers of snowshoe hares declined, emigration and mortality rates increased in floaters before territory owners were affected. The results of this study show how a large proportion of secretive floaters can delay the detection of population declines in traditional censuses of territorial birds, and can lead to serious underestimates of the impacts of predation.

Non-territorial 'floaters', which live a secretive life and form a 'shadow population', are well known for some bird species and assumed for many others (Brown 1964, Newton 1992, Smith 1978, Watson and Moss 1970). Sometimes, such 'surplus' birds live in areas separate from breeding territories, and they may become directly observable when they form social groups (Birkhead *et al.* 1986, Charles 1972) or they may be detectable in open habitat (Haller 1996, Hannon and Martin 1996, Jenny 1992, Watson 1985). Most of the knowledge about floaters, however, is indirect and is derived from experimental removals of territory holders (review in Newton 1992). The majority of owl species are territorial, and ecological field studies are usually based on territorial birds. Very little is known about floaters in territorial owl populations.

The question of why some birds in a population do not establish a territory and do not breed has been approached from several directions. One hypothesis suggests that the social behavior of territory holders prevents them from breeding (review in Newton 1992). Another hypothesis suggests that a non-territorial stage in an individual's life is not the fate of 'doomed surplus' birds, but is an alternative strategy leading to higher fitness than the strategy of breeding early (Smith and Arcese 1989). Two elements could be involved in such a strategy: (i) Life history theory predicts a trade-off between current investment and future survival, and delayed maturation may be particularly successful for long-lived species such as many owls, because they would produce offspring later in life when they are more experienced and have more secure access to resources

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(review in Stearns 1992). (ii) Delayed establishment of a breeding territory is not necessarily an inactive period in reproduction. Male floaters may gain extra-pair copulations without the cost of defending a territory and providing the brood, whereas female non-territorial owls may secretively settle as a secondary mate of a territorial male of high quality (reviews in Birkhead and Møller 1992, Møller 1987, Korpimäki 1988, Korpimäki *et al.* 1996).

How do floaters survive in a territorial owl population? Very little is known about the behavior of non-territorial owls. How vagrant are they? Do they overlap in their space use with territorial owls or are they restricted to undefended habitat? Do they have special behaviors to avoid aggression by territory owners, and how dangerous it is to intrude into defended space? What is the foraging behavior of non-territorial owls, where do they obtain their food, and how do their intake rates compare to territory owners?

Finally, the question of how many floaters live in a territorial owl population arises. Because territorial owls are easier to detect than floaters, most ecological studies on owls are restricted to the territorial fraction of a population. The consequences of varying floater populations are particularly relevant to predation studies, which may underestimate the effects of owls as predators, and to conservation studies, because a pool of non-territorial birds can affect the recovery of populations (Newton 1991) or can mask population declines when census data is based on breeding territories (Franklin 1992, Wilcove and Terborgh 1984).

I studied Great Horned Owls *(Bubo virginianus)* in the boreal forest in the southwest Yukon, Canada. Great Horned Owls are large, long-lived predators feeding mainly on lagomorphs (Donazar *et al.* 1989). They are territorial year-round, and are widely distributed across North and South America (Voous 1988). Occasional irruptions of Great Horned Owls into southern Canada and the northern United States are linked to the decline phase in the 10-year population cycle of snowshoe hares *(Lepus americanus* Erxleben), which is synchronized across boreal Canada and Alaska (Adamcik *et al.* 1978, Houston 1987, Houston and Francis 1995, Keith and Rusch 1989, McInvaille and Keith 1974, Rusch *et al.* 1972).

The goal of this paper is to present a portrait as comprehensive as possible of floaters in a selected owl species, and to encourage further studies on floaters in territorial owl populations.

METHODS

This study was part of a collaborative project on the dynamics of the boreal forest ecosystem (Krebs *et al.* 1995). We worked at Kluane Lake (60° 57'N, 138° 12'W) in the southwestern Yukon, and our study area comprised 350 km^2 of the Shakwak Trench, a broad glacial valley bounded by alpine areas to the northwest and southeast. The valley bottom averages about 900 m above sea level and is covered mostly with spruce forest *(Picea glauca* Blake), shrub thickets *(Salix* L. spp.), some aspen forest *(Populus tremuloides* L.), grassy meadows with low shrub *(Betula glandulosa* Raup.), old burns, eskers, marshes, small lakes, and ponds.

The population data of Great Horned Owls span the years 1988-1993, while most other data are from 1989-1992. Great Horned Owls were censused in late winter and early spring on a 100 km^2 plot within the main study area. Individual pairs were identified when hooting simultaneously with neighbors at dawn and dusk, and obvious disputes between hooting males or pairs were used for the mapping of territorial boundaries. When necessary, playbacks of calls were used to elicit territorial responses of owners and their neighbors. Most males were individually known, not only because of radio-tagging but also because of their distinctly different hoots. These differences were later verified with sonograms from recordings at the nest (unpubl. data, method as used for *Strix aluco* by Galeotti 1990). Observations of territorial activity were made almost daily from early February until late April (at least 300 hours in each year).

Survival estimates and information on movements were based on individual Great Horned Owls monitored by radio-telemetry. Twenty-one territorial adult owls were captured with mistnets and cage-traps, and 55 owlets were equipped with radio-transmitters before fledging (breakdown of sample sizes in Rohner 1996, 1997). Successful dispersers were later monitored intensively (3 hatched in 1988, 11 in 1989, and 16 in 1990), and 9 remained as non-territorial floaters in the study area. The radios weighed 50 g including a shoulder harness of teflon ribbon for attachment as a backpack (< 5 percent of body weight, Kenward 1985). Battery life was 2-2.5 years. The radios were equipped with a two-phase activity switch (sensitive to movement and change of angle).

All floaters and territory holders with transmitters were normally monitored once per week (for the presentation of weekly data, locations in addition to the weekly sampling intervals were excluded). Most checks were conducted with hand-held equipment from the Alaska Highway, which follows the valley bottom for the whole length of the study area. In addition, the entire area and its surroundings were searched for radio signals from helicopter or fixed-wing aircraft at least twice per year (in fall after dispersal, and in spring after the onset of breeding).

Telemetry locations were obtained by triangulating owls with hand-held equipment. Topographical maps were used in the field to plot the locations and assess the number of bearings needed for reliable estimates. The triangulations were then analyzed with the program "Locate II" (Nams 1990) for calculating exact locations and distances. Details on median 95 percent-error ellipses (Lenth estimator, Saltz and White 1990) are presented in Rohner (1997). The accuracy of telemetry locations was assessed by triangulating five transmitters that were placed in trees at a height of 4.5-5.5 m. The deviation of these telemetry locations (error area of 0.052 ± 0.018 km^2) from the site coordinates obtained by GPS (Global Positioning System) was 0.101 ± 0.027 km.

Home ranges were measured by utilization distributions based on clustering methods, and all calculations were performed using the program "Ranges IV" (Kenward 1990). From a center of closest locations, an increasing percentage of nearest-neighbor locations were added, resulting in a cumulative increase of core area used. Mononuclear clustering was centered around the harmonic mean location only, whereas multinuclear clustering allowed for separate clusters of closest locations. Home range sizes were then derived for different levels of core percentages (Kenward 1987). For the monitoring period in September 1991, three territorial owls were excluded from analysis because of extreme long-distance movements during several days (these extra-territorial movements are described in Rohner 1996).

All arithmetic means are reported with standard errors and all probabilities are two-tailed unless otherwise specified. Correlation coefficients were calculated as Spearman rank correlations. For statistical testing, nonparametric tests were used wherever possible. The testing of bootstrap hypotheses followed the guidelines of Hall and Wilson (1991), and two-sided probabilities were derived from 500 simulations (see also Rohner 1996).

RESULTS

Dispersal of Juveniles and Age at Maturity

Juvenile owls stayed in their natal territories until September, and then rapidly dispersed in the following weeks (table 1). Dispersal dates were delayed when the cyclic population of snowshoe hares started to decline in 1991 ($U = 152$, $p = 0.01$). By the end of the first week in October 1989 and 1990, only 4 percent (1 of 27) were still in their natal territories. (In 1991, three of seven owls had not left their natal territories by that time but never dispersed and died in the subsequent winter months near where they fledged). Dispersal distances were not significantly different between years (table 1). Of 55 fledglings monitored from 1988-1991, 29-45 percent remained within 35 km of their natal territories. This distance is equivalent to 10-15 territories in diameter.

The long life spans of radio-transmitters allowed us to examine the integration of fledglings into the breeding population. Only 15 percent (3 of 20) settled in territories before the end of their first year of life. None of nine owls that were further monitored to the end of their second year of life settled during that time. Because of the scarcity of such data, some details are given on the three fledglings that became territorial within the study area: In 1988, one female out of three monitored yearlings, settled in late spring 1989, was actively territorial in fall 1989, and bred successfully in 1990 and 1991. In 1990, two female siblings settled immediately in the same fall without any of the extended dispersal movements typical of other radio-tagged juveniles. Both of these siblings fledged young in the following spring.

Hooting Activity

The remaining 85 percent of monitored owls ($n = 20$), which had not settled within 2 years

Table 1.—*Dispersal of juvenile Great Horned Owls (*Bubo virginianus*) at Kluane Lake, Yukon (Rohner 1996). Data are provided for sample sizes, dispersal dates, median dispersal distances from the nest in early September (2-9 Sept.) and mid-October (14-21 Oct.), and the proportion of juveniles <35 km from their natal territories by the following spring (either becoming territory holders or remaining floaters).*

	1989	1990	1991
Juveniles monitored	11	16	7
Earliest dispersal date	13 Sept	2 Sept	17 Sept
Latest dispersal date	5 Oct	15 Oct	n.a.
Median dispersal date	20 Sept	20 Sept	27 Sept
Dispersal early Sept. (km)	0.6	0.7	0.8
Dispersal mid Oct. (km)	30.6	35+	16.0
Proportion dispersing < 35 km	.45	.37	.29

after dispersal, did not show any sign of hooting or other territorial defense. In order to test whether these non-territorial 'floaters' would normally be included in a census, a number of radio-tagged owls were monitored within hearing range to record their hooting activity from 3 March to 27 April 1990. Hooting activity was measured as the duration of bouts, each of them considered to be finished when more than 5 minutes elapsed between hoots.

Almost all territorial males, and often also females, gave territorial challenges at least for a short time, particularly at dusk and dawn (see also Rohner and Doyle 1992). In 11 territories that were monitored for a total of 32.0 hours between dusk and midnight, all males were recorded giving territorial challenges. Their hooting bouts lasted 26.7 percent of the total time. Of six individual floaters that were monitored for a total of 16.8 hours between dusk and midnight, none of them gave a territorial challenge or any other call.

During the same time period, known territorial and non-territorial owls were tested for their responsiveness to playback. Territorial challenges were broadcast at irregular intervals for a total duration of 20 minutes from a tape-recorder, and each individual was tested in one trial. Seventeen out of 24 territorial males (70.8 percent) responded vocally. Two out of six floaters approached the speaker as concluded from telemetry readings, but none of them responded with a vocal signal that would have allowed their detection during a standard census (Fisher's Exact Test, $P < 0.01$, $DF = 1$, $n = 30$).

Movements and Residency of Floaters

The movement patterns of territory holders and floaters were substantially different. Territorial owls were extremely restricted in their movements, and distances between weekly locations of > 3 km were exceptional (calculating median weekly movements for each territory owner, the median over these values for 18 birds was 0.95 km). With a median of 2.63 km, the weekly movements of eight floaters were greater than those of 18 territorial owls ($U = 137$, $p < 0.001$, $n = 26$). Non-territorial owls showed a variety of movement patterns involving larger excursions but were overall relatively sedentary (fig. 1). Only about 20 percent of the recorded distances were greater than 10 km from 1 week to another (Rohner 1996), and none of the radio-marked owls became transient floaters that seemed to move continuously through a large region (fig. 2). Typically, a floater would move within an area of about 5-6 times the size of a territory, and then shift to another area over time, sometimes switching between several known areas of similar size (further details on shifts and patchiness in space use in Rohner 1997).

Size of Home Ranges

Based on weekly locations, floaters covered a 90 percent-area of 12.0-48.3 km^2 in 1990 and

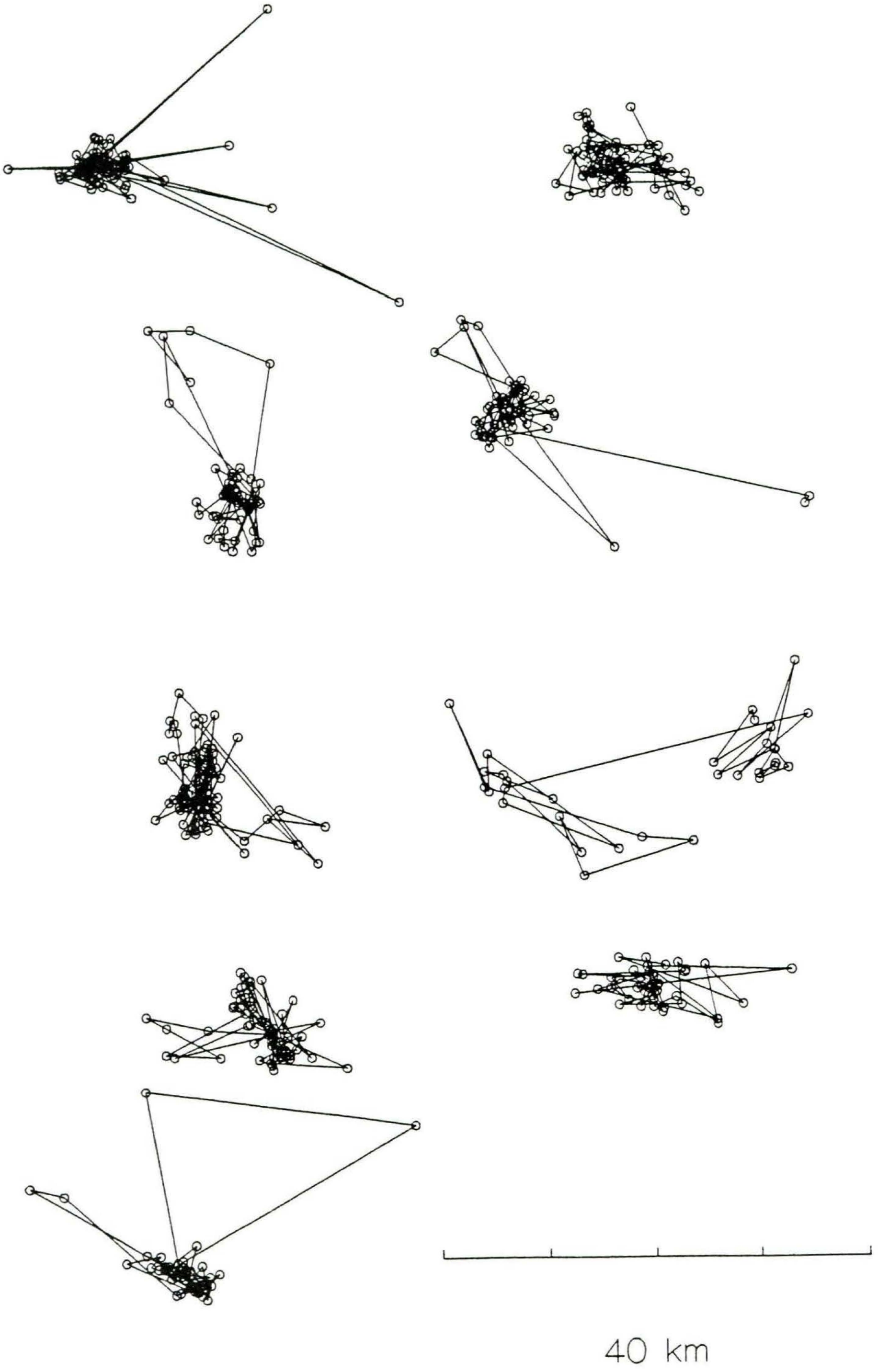

Figure 1.—*Weekly locations of nine non-territorial Great Horned Owls (*Bubo virginianus*) during 1990-1992 at Kluane Lake, Yukon (Rohner 1997). The birds are arranged in a panel with the original scale and topographical x-y orientation maintained.*

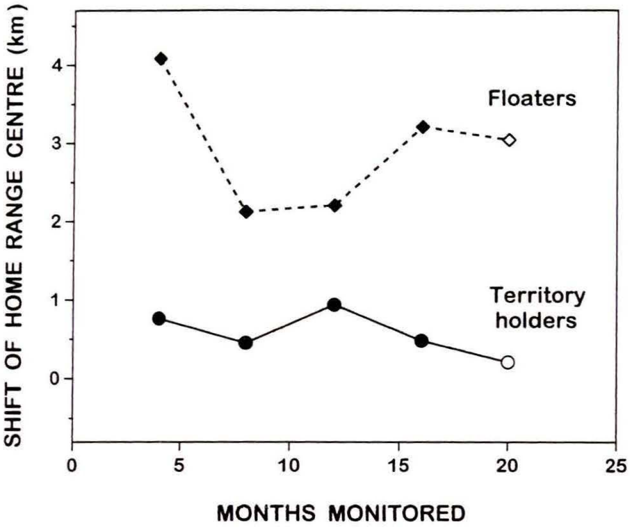

Figure 2.—*Median shifts of home range centers, based on all locations, between subsequent 4-month periods of monitoring of floaters and territorial Great Horned Owls (*Bubo virginianus*) at Kluane Lake, Yukon (Rohner 1997). Filled symbols represent significant differences between the social classes (Mann-Whitney $p<0.05$). Sample sizes for the time periods were n_1=8,8,7,6,4 floaters and n_2=10,8,8,5,1 territorial owls.*

4.75-69.4 km² in 1991. On average, these values were 26.1 ± 5.7 km² and 24.8 ± 8.1 km². The differences between the 2 years were not significant for 90 percent-area or any other core percentages (Mann-Whitney U = 24-37, p = 0.09-1.00, $n_1 = 6$, $n_2 = 8$), and the differences were not consistent in any direction for a subsample of individuals that were monitored through both years (Wilcoxon paired rank-test, Z = 0.94, p = 0.34, n = 5).

Defended territories were much smaller than floater home ranges. In 1990, there were 18-19 territorial pairs per 100 km² (Rohner 1996), i.e., an average territory size of 5.26-5.56 km². In 1991, the boundaries of 16 territories were mapped by observing encounters of hooting males. Territory sizes ranged from 2.30-8.83 km², with an average of 4.83±0.40 km².

A more direct comparison of space use between territorial and non-territorial owls consisted of a 3-week period in September 1990 and 1991 with locations for each night. Several measures of home range sizes are presented in table 2. Floaters had significantly larger 90 percent-areas (based on both mononuclear and multinuclear analysis); the multinuclear 70 percent-areas were not significantly different.

Reproductive Status of Non-territorial Owls

Floater movements and home ranges showed no consistent changes during courtship and egg-laying by territorial birds in February and March, as would be expected if male floaters seeked extra-pair copulations or females settled on broods as secondary females. During 3 weeks of this fertile period for females in 1991 (see Rohner 1996), home range sizes were 7.72 ± 1.48 km² for the mononuclear 90 percent-area, 4.11 ± 2.16 km² for the multinuclear 90 percent-area, and 0.68 ± 0.15 km² for the multinuclear 70 percent-area. The daily movements were 1.309 ± 0.217 km *vs* 1.431 ± 0.124 km in the periods of September 1990 and 1991 (p = 0.37, Mann-Whitney U = 12, $n_1 = 5$, $n_2 = 7$).

Table 2.—*Home range sizes of territorial and non-territorial Great Horned Owls (*Bubo virginianus*) during a 3-week period in September 1990 and 1991 at Kluane Lake, Yukon (one location per night, Rohner 1997). Sample sizes (a-b), three different measurements of home range size (c-e). are presented. Probabilities refer to the Mann-Whitney U-Test (two-sided).*

	Variable	Floaters	Territory owners	P
1990/91	(a) N owls	7	10	
	(b) N locations/owl	18.7 ± 1.0	20.0±0	
mononuclear:	(c) 90%-area	7.25 ± 1.35 km²	248.4 ± 41.4 km²	0.002
multinuclear:	(d) 90%-area	4.68 ± 1.16 km²	103.2 ± 15.9 km²	0.011
	(e) 70%-area	0.56 ± 0.14 km²	0.24 ± 0.04 km²	n.s.

None of the birds settled on nests as secondary females of territorial males.

Territorial Behavior and Floaters

The home ranges of non-territorial owls overlapped broadly those of other owls of the same social class (fig. 3). On average, mononuclear 90 percent-areas overlapped by 23.3 ± 4.8 percent and multinuclear 90 percent-areas overlapped by 28.8 ± 6.4 percent (n = 23 overlappers and n = 18 over-lappers respectively, only for combinations of floaters that were monitored simultaneously and had > 1 percent overlap). There were no consistent differences between 1990 and 1991. Some overlapped with up to four other monitored floaters (fig. 3), and the highest overlap observed with one other floater was 87.8 percent (mononuclear 90 percent-area in 1991).

Floaters were not restricted to areas outside of established territories and intruded widely into several territories (all mononuclear 90 percent-ranges of figure 3 overlapped with at least five territories in the area of figure 4 where territorial boundaries were known). On a finer scale, however, some spatial segregation became apparent (fig. 4). Four of five floaters were located significantly closer to territorial boundaries than expected from a random pattern (table 3). The median distance of random points to territorial boundaries was 0.343 km, the overall median of the results for individual floaters (not the median of the pooled data) was 0.229 km. This deviation of 33 percent was significantly different from random (bootstrap P < 0.001).

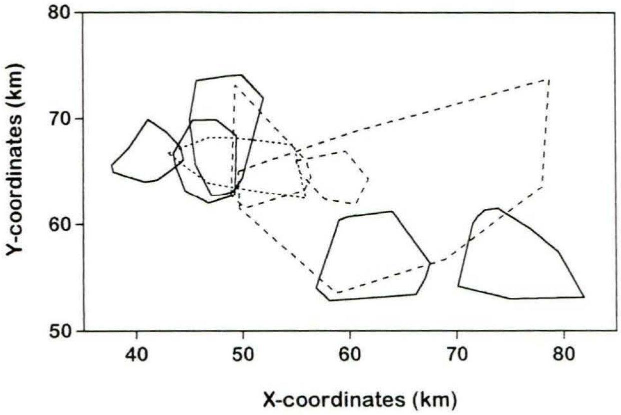

Figure 3.—*Spatial overlap among non-territorial Great Horned Owls (*Bubo virginianus*) at Kluane Lake, Yukon (Rohner 1997). The home ranges presented are based on 90 percent-areas calculated by mononuclear clustering. Five owls monitored both in 1990 and in 1991 are identified by solid lines, one owl monitored only in 1990 by a broken line, and three owls monitored only in 1991 by dashed lines.*

The hypothesis that territorial behavior limits population density can be tested by removal experiments (e.g., Newton 1992). While monitoring radio-marked Great Horned Owls, I observed six vacancies in territories which served as natural removal experiments (table 4). Territory holders either died or emigrated, and I recorded whether these vacancies were filled with new birds. In at least five of six vacancies, such replacements occurred. None of these owls were known territorial owls from the study area. In case two, it was unclear if the territory holder had been replaced or not. (Because it was often difficult to observe successful replacements, and because checks were made opportunistically, the dates when new territory holders were confirmed do not necessarily reflect the accurate time of replacement. The estimated intervals should therefore be considered upper limits of the real intervals.)

The hypothesis of social exclusion by territorial behavior was consistent with the result of density-dependent parameters in population growth. The number of established owl territories increased throughout 1988-1992 in response to a cyclic peak of snowshoe hares, but this yearly increase declined towards higher densities of pairs already present (fig. 5a). Although the sample size of only 4 years is small, the negative slope of the regression is significant ($y = 1.67 - 0.03x$, $r^2 = 0.95$, $p < 0.05$). As the number of established owl pairs increased and territories were packed more densely in the study area, not only the addition of further territories was reduced but also the floater pool increased strongly (fig. 5b, $y = 3.89x - 44.84$, $r^2 = 0.96$, $p < 0.05$; details in Rohner 1995).

Size of the Floater Population

The density of non-territorial floaters was estimated based on a population model including productivity, survival, and emigration (details in Rohner 1996). At peak hare densities, reproductive success and juvenile survival

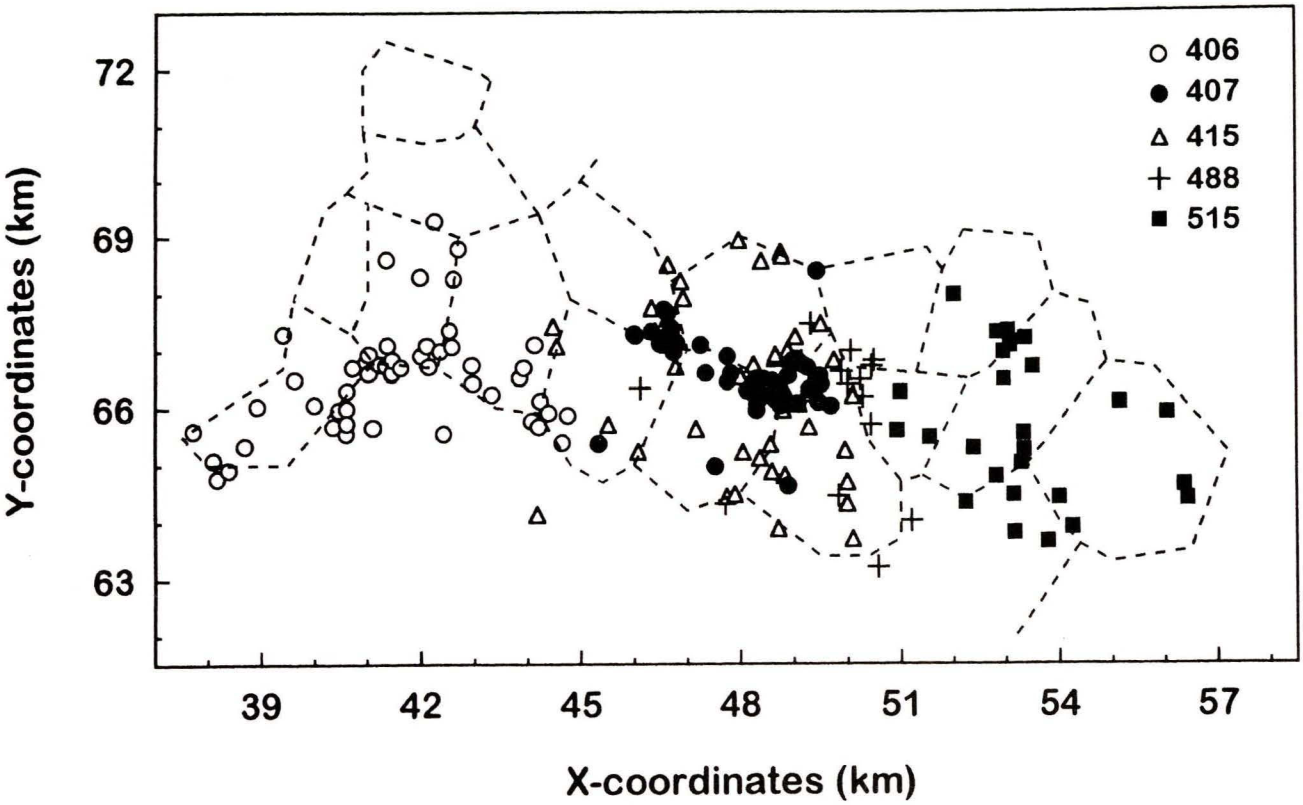

Figure 4.—*Locations of Great Horned Owl (*Bubo virginianus*) floaters relative to territorial boundaries, during the period of September 1990 to June 1991 at Kluane Lake, Yukon (Rohner 1997). Five individual floaters (see table 3) are represented with different symbols and a total of 198 locations. All locations are shown within the minimum convex polygon that connects the outermost corners of these known territories. Less precise locations with 95 percent-error areas <70.5 km² were excluded.*

Table 3.—*Distances of floater locations relative to the boundaries of territorial Great Horned Owls (*Bubo virginianus*) from September 1990 to June 1991 at Kluane Lake, Yukon (locations with 95 percent-error area <0.5 km² and within the territories shown in fig. 6). For bootstrapping probabilities, the results from actual locations were compared to those from locations that were randomly distributed within the outermost boundaries of these territories (median distance of random points to territorial boundaries 0.343 km, quartiles 0.185-0.547 km).*

N	Individual	Median (km)	Quartiles (km)	P
30	406	0.229	0.125-0.350	0.05
56	407	0.214	0.119-0.355	0.002
40	415	0.232	0.138-0.450	0.018
16	488	0.163	0.142-0.254	0.006
22	515	0.344	0.125-0.482	0.958
164	Pooled	0.222	0.130-0.381	<0.001

Table 4.—*Natural removal experiments and replacements of radio-marked territorial Great Horned Owls (*Bubo virginianus*) at Kluane Lake, Yukon (Rohner 1996).*

Sex	Estimated vacancy	Cause	Replacement confirmed	Interval to replacement
1. Female	10 Jul 1989	mortality	04 Dec 1990	ca. 4 months
2. Female	28 Jun 1991	mortality	-	?
3. Female	20 Nov 1991	mortality	12 Mar 1992	< 3.5 months
4. Male	25 Jan 1992	mortality	10 Mar 1992	< 7 weeks
5. Female	01 Feb 1992	emigration	12 Mar 1992	< 3 weeks
6. Female	26 Feb 1992	mortality	11 Mar 1992	< 6 weeks

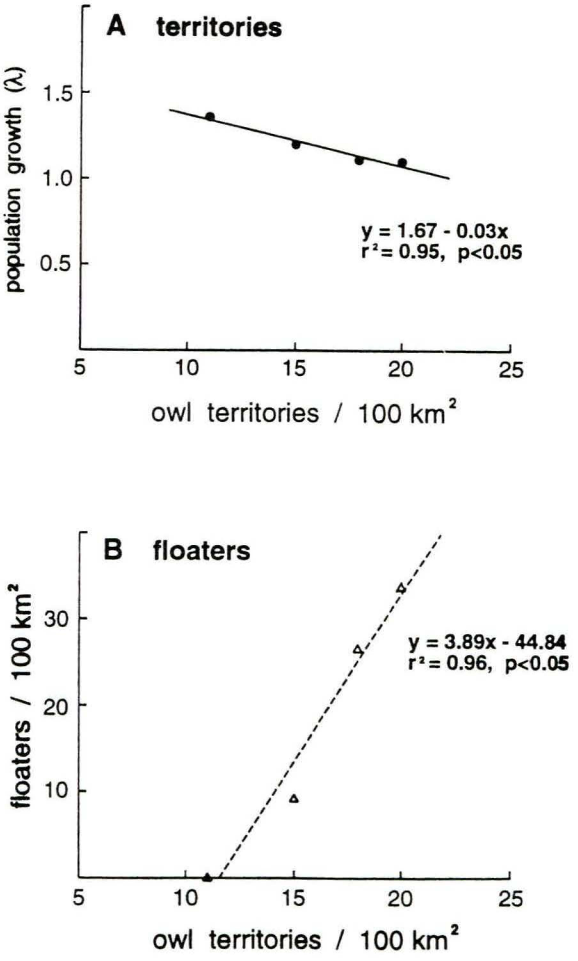

Figure 5.—*Social behavior and the limitation of population growth in Great Horned Owls (*Bubo virginianus*) at Kluane Lake, Yukon (Rohner 1995).* ***A:*** *Growth rates of the territorial population decline as numbers of owl territories increase in the area (inverse density-dependent growth rate).* ***B:*** *Numbers of non-territorial 'floaters' increase as territories are packed more densely (density-dependent increase).*

were very high (Rohner 1996, Rohner and Hunter 1996), therefore leading to large cohorts of dispersing juveniles in autumn. Weekly monitoring of radio-marked owls resulted in interesting differences in survival and emigration between floaters and territory owners (fig. 6). Survival was extremely high during the hare peak and emigration was negligible for both social classes. As the prey base declined, floaters were negatively affected before territorial birds (fig. 6). These differences were statistically significant (table 5).

The results of integrating these demographic parameters are presented in fig. 7a. Even when assuming that no floaters were present in spring 1988 for a minimum estimate, the numbers rose quickly from zero to densities similar to territorial owls (fig. 7b). The beginning of the hare decline in the winter of 1990/91 resulted in an immediate reduction in population growth due to emigration and lowered production of recruits by territorial pairs. Floater densities reached a peak with a time lag of 1 year relative to the hare cycle, and then dropped sharply from 1991 onwards, because of increased emigration and mortality, and because no additional juveniles were produced locally that could have compensated for losses in the non-territorial segment of the population.

The number of territorial owls in the study area increased almost linearly from 1988-1992 (fig. 7b, census data). Even when the hare population started to decline in 1990/91, the number of owl territories kept rising until spring 1992. Then, with a time lag of 2 years relative to the hare cycle, the number of territories dropped in 1993.

The numerical response of the total population of Great Horned Owls is given in figure 7b.

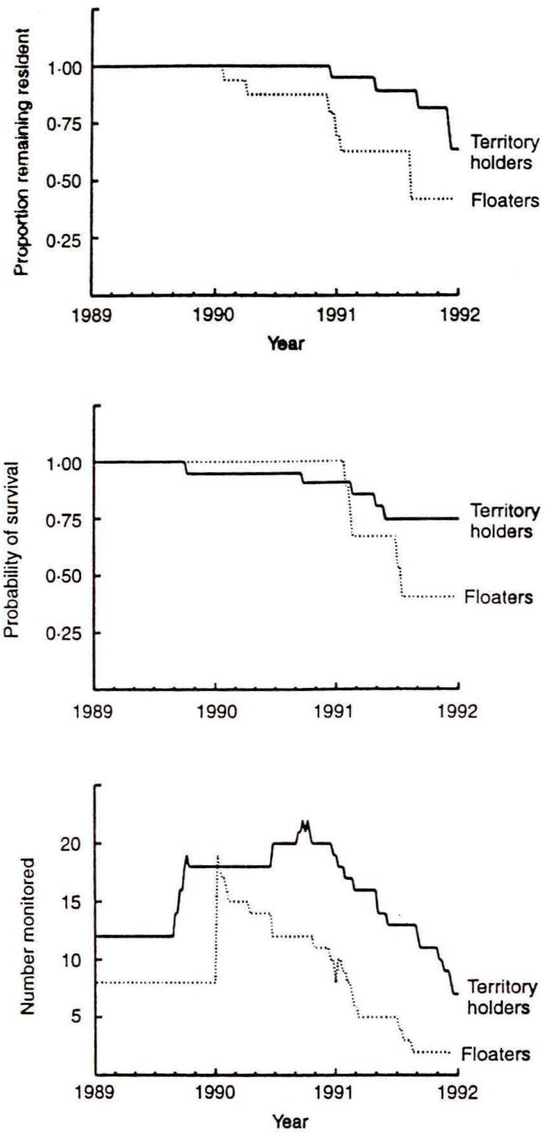

Figure 6.—*Survivorship and emigration of adult Great Horned Owls (*Bubo virginianus*) (territory holders) and young owls (first and second year, floaters) based on radio-telemetry at Kluane Lake, Yukon (Rohner 1996).* ***A:*** *'Residency rate' (1 meaning all owls remain resident, 0 meaning all owls emigrate).* ***B:*** *Probability of survival;* ***C:*** *Number of owls monitored. Years begin and end in early October.*

Since the territorial segment represented a nearly linear component, the sum of densities or overall pattern more closely resembled the floater response with (a) an immediate reduction in population growth as hare densities declined, and (b) with a decline that was delayed by 1 year relative to the hare cycle.

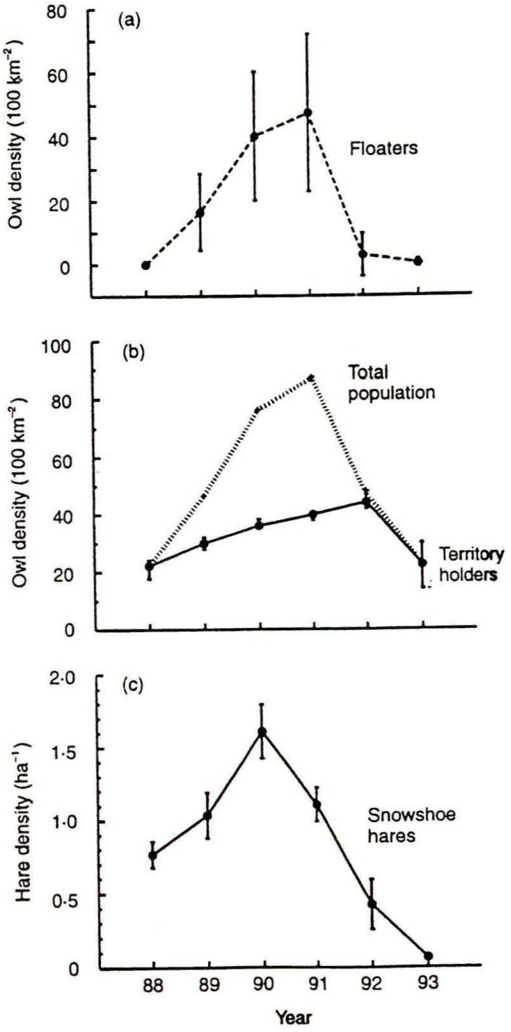

Figure 7.—*Numerical response of Great Horned Owls (*Bubo virginianus*) (spring densities) to the snowshoe hare cycle at Kluane Lake, Yukon (Rohner 1996).* ***A:*** *Estimated density of non-territorial owls ('floaters').* ***B:*** *Census of the territorial population (with minimum and maximum estimates), and total population (sum of territorial and non-territorial owls).*

DISCUSSION

How Do Floaters Live in a Territorial Owl Population?

Non-territorial Great Horned Owls were not transient floaters that occurred at specific sites for only short periods of time. They used fairly stable home ranges with a space use similar to that of territorial Great Horned Owls. The most striking difference was in home range size.

Table 5.—*Survival and emigration of Great Horned Owls (*Bubo virginianus*) at Kluane Lake, Yukon, as determined by radio-telemetry from fall 1989 to fall 1992 (Rohner 1995). Given are yearly survival rates (s_{Ti} and s_{Fl}), and yearly 'residency rates' (e_{Ti} and e_{Fl}), for territorial owls and floaters. Survival rates are (1-mortality), residency rates are (1-emigration). All rates (including overall calculations) are annual rates.*

Time period	Hare densities	Social class	Survival ± SE	Residency ± SE	N monitored total (weekly avg.)
1989-1990	peak	territorial	.947±.051	1.000	19 (14)
		floater	1.000	1.000	8 (8)
1990-1991	1st yr decline	territorial	.955±.047	.950±.049 [1]	22 (19)
		floater	1.000	.696±.136 [1,2]	19 (13)
1991-1992	2nd yr decline	territorial	.819±.132 [1]	.668±.136 [2]	18 (13)
		floater	.400±.219 [1,2]	.600±.268	10 (4)
1989-1992	overall	territorial	.905±.073	.860±.136	22 (16)
		floater	.701±.174	.748±.225	19 (8)

[1] $p<0.05$ for difference between social classes (within individual years).

[2] $p<0.05$ for difference to previous year (within social classes).

Based on weekly locations per year, floaters covered an area roughly five times the size of an average owl territory. Although floaters left more frequently for long-distance excursions and therefore were more flexible in seeking out opportunities, they shifted home range centers only 2-5 times more than territory owners. Much of this difference may be explained by the larger home ranges of floaters and an initially unstable phase when young floaters settle. Non-territorial Great Horned Owls were certainly not nomads using resources entirely opportunistically and free of spatial attachment (see also Rohner and Krebs 1997).

Why are floaters not more nomadic? One explanation may lie in the evolutionary design of forest owls (Martin 1986, Norberg 1987). Spatial knowledge may be paramount to hunting success in a highly structured habitat, particularly when information is incomplete in the dark, and may lead to conservative use of space ('nocturnal syndrome', Martin 1990; see also Rohner and Krebs 1996, Stamps 1995). An optimal hunting strategy may minimize space use, but floaters could be forced to use larger home ranges and choose hunting sites more opportunistically, simply because some of these sites are unavailable when occupied by territory owners. How familiarity with an area affects hunting success and mate acquisition remains to be studied.

Little is known how social behavior affects non-territorial owls, and the information available is usually restricted to evidence for the presence of non-territorial floaters (Austing and Holt 1966, Franklin 1992, Hirons 1985). Floating owls in our study were extremely secretive. They were never observed to vocalize and did not respond to playback of territorial calls. Floaters overlapped in their space use with each other, and seemed to move independently of each other. They did not concentrate in areas separate from territory holders but overlapped broadly with the occupied territories in the study area. At a finer scale, nevertheless, they were located more frequently along territorial boundaries than expected by chance. To my knowledge, this is the first direct evidence that territorial behavior can restrict the space use by floaters in owls.

Details of how non-territorial owls hunt in defended territories or how frequently they interact with owners aggressively, are unknown. In the study area, we found four Great Horned Owls that may have been killed by other Great Horned Owls. On one of those carcasses, a Great Horned Owl was seen, and owl footprints in the snow were observed at a second (F. Doyle, pers. comm.). Fatal fighting can evolve when a major part of a contestant's lifetime reproductive success is at stake (Enquist and Leimar 1990). This, for example, may occur in saturated populations of Golden Eagles (*Aquila chrysaetos*) (Haller 1996). Many diurnal raptors have conspicuous immature plumages (Newton 1979) and display this bright coloration to approaching territory owners (Jenny 1992, pers. comm.). Such ritualized encounters may be more difficult in the dark, and it would be interesting to know the cost of being detected for an intruding floater, and which behavioral mechanisms floaters may use to reduce the risk of detection and injury. Although much work has confirmed that territorial males recognize the songs of their neighbors (e.g., Falls 1982), little attention has been paid to the possibility that non-territorial birds may use mental maps of territory boundaries plus the identification of the spatial distribution of singing males to assess their risk of detection when intruding into a territory.

Why Not Defend a Territory?

Is delayed maturation in owls an evolutionary strategy with higher fitness than breeding early? The results of this study do not support this hypothesis (see also Smith and Arcese 1989, Stearns 1992). Although very few young birds settled in territories during the first 2 years of their life despite peak populations of prey, three of the monitored owls proved that Great Horned Owls are capable of reproducing at the end of their first year of life. Large owls of the genus *Bubo* (L.) and *Nyctea* (L.) are known to breed as yearlings in captivity (Flieg and Meppiel 1972, K. McKeever, pers. comm.), but the age at first breeding in natural populations has only been speculated on (Adamcik *et al.* 1978, Henny 1972, Weller 1965). My observations of Great Horned Owls breeding as yearlings are the first to my knowledge. All of these birds were females. Earlier onset of breeding in females than males may represent a typical pattern, because both in owls and other raptors males establishing new territories are the sole providers of food for the female and the young throughout most of the breeding period, which may be more difficult than joining a male in a new territory and laying and incubating eggs (Newton 1979).

Is floating an alternative strategy with higher fitness because of opportunities for reproduction without the cost of territorial defense? Non-territorial females could attempt to breed as secondary females once the primary female is incubating (Korpimäki 1988). Although I spent considerable effort attempting to document such cases, polygyny was never discovered, even during such extreme prey densities. Incubating females left their nests on several occasions to join hooting males at the territorial boundary, and I propose that territorial females prevent other females from settling. Such sex-specific defense has been demonstrated for Magpies *(Pica pica)*, another species where long-term territories are occupied by a monogamous pair (Baeyens 1981).

Reproductive activity is more difficult to demonstrate for male floaters. There was no obvious change in movement patterns of floaters during the fertile period of females, suggesting that floater males did not become 'satellites' of territorial pairs in pursuit of opportunities for extra-pair copulations (Møller 1987). This, however, does not rule out that floater males reproduced. Floaters overlapped with territories, and an observation in Flammulated Owls *(Otus flammeolus)* showed that an extra-pair copulation can occur within a short duration and without any prior vocalizations (Reynolds and Linkhart 1990). Evidence for extra-pair copulations, however, has yet to be shown by further studies involving DNA analysis. Extra-pair paternity may be rare in diurnal raptors (review in Korpimäki *et al.* 1996), whereas the situation is basically unknown for owls. First results for Tengmalm's Owls (*Aegolius funereus*) (E. Korpimäki *et al.*, unpubl. data) suggest that extra-pair fertilizations may also be rare in strigiforms.

There is increasing evidence that territorial behavior can restrict the breeding activities and the establishment of territories in birds, and therefore can limit population growth (review in Newton 1992). In several bird species, aggressive encounters between territory holders and intruders, or the presence of non-breeding flocks have been noted. There is little evidence, however, for an effect of territorial behavior on the distribution of floaters particularly in forests (e.g., Arcese 1987, Matthysen 1989). The fact that floaters were located more often at the periphery of established territories does not prove that territoriality excluded these floaters from breeding (Watson and Moss 1970). Nevertheless, all results of this study including the presence of non-territorial birds capable of reproduction, replacements of territorial vacancies, reduced growth of the territorial population and accumulation of floaters as territories became more packed, all support the hypothesis that territorial behavior excluded floaters from establishing territories and from breeding (see also Rohner 1995, Rohner and Smith 1996).

CONCLUSIONS

Floaters in Great Horned Owls were secretive and would not have been detected by standard censuses. During a cyclic peak of snowshoe hares, their numbers were estimated to reach 40-50 percent of the territorial, and therefore visible population. This raises some serious concerns for ecological and conservation approaches. For example, many studies have attempted to quantify the effect of predators on prey populations. In my case, the predation pressure on prey would have been severely underestimated if traditional censusing methods had been used. The notion of large floating populations may lead to a cautious interpretation of previous results, and may perhaps give incentives for expanded censusing techniques.

For conservation efforts, it is important to recognize territorial behavior as a dynamic component of populations. The age of floaters and their breeding potential are relevant to how natural populations respond to environmental change (Caughley 1977; Lande 1988; Newton 1991, 1992; Perrins 1991; Sinclair 1989). If floaters can breed, but are prevented from doing so by territory holders, they add flexibility to the dynamics of a territorial population. For example, the rapid increase of a population of Sparrowhawks *(Accipiter nisus* L.) recovering from high pesticide levels was possible because of high recruitment of young birds into the breeding segment of the population (Wyllie and Newton 1991).

This also raises a serious concern for conservation. When, as here, floaters are more affected by decreasing habitat quality than territorial birds, traditional monitoring programs that are based on censusing territories will not reveal these declines at an early stage (Wilcove and Terborgh 1984). In a scenario for slowly declining Spotted Owl populations, Franklin (1992) estimated that declines in territorial owls could not be detected for 15 or more years when floaters were present even at low densities.

Little is known about the size and structure of floater populations (Matthysen 1989, Newton 1992, Smith 1978, Smith and Arcese 1989). At present, it is unclear to what degree these results also apply to non-cyclic owl populations. Further research on the mysterious life of non-territorial owls is strongly encouraged.

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LITERATURE CITED

Adamcik, R.S.; Todd, A.W.; Keith, L.B. 1978. Demographic and dietary responses of Great Horned Owls during a snowshoe hare cycle. Canadian Field-Naturalist. 92: 156-166.

Arcese, P. 1987. Age, intrusion pressure, and defense against floaters by territorial male song sparrows. Animal Behavior. 35: 773-784.

Austing, G.R.; Holt, J.B. 1966. The world of the Great Horned Owl. New York: Lippincott.

Baeyens, G. 1981. The role of the sexes in territory defense in the Magpie. Ardea. 69: 69-82.

Birkhead, T.R.; Eden, S.F.; Carkson, K.; Goodburn, S.F.; Pellatt, J. 1986. Social organization of a population of Magpies *Pica pica*. Ardea. 74: 59-68.

Birkhead, T.R.; Møller, A.P. 1992. Sperm competition in birds. London: Academic Press.

Brown, J.L. 1964. The evolution of diversity in avian territorial systems. Wilson Bulletin. 76: 160-169.

Caughley, G. 1977. Analysis of vertebrate populations. New York: John Wiley.

Charles, J.K. 1972. Territorial behavior and the limitation of population size in crows, *Corvus corone* and *C. cornix*. Scotland: University of Aberdeen. Ph.D. dissertation.

Donazar, J.A.; Hiraldo, F.; Delibes, M.; Estrella, R.R. 1989. Comparative food habits of the Eagle Owl *Bubo bubo* and the Great Horned Owl *Bubo virginianus* in six palearctic and nearctic biomes. Ornis Scandinavica. 20: 298-306.

Enquist, M.; Leimar, O. 1990. The evolution of fatal fighting. Animal Behavior. 39: 1-9.

Falls, J.B. 1982. Individual recognition by sounds in birds. In: Kroodsma, D.E.; Miller, E.H., eds. Acoustic communication in birds. London: Academic Press: 237-278.

Flieg, G.M.; Meppiel, P.R. 1972. An account of trio nesting by yearling Snowy Owls in captivity. Journal of Raptor Research. 6: 103.

Franklin, A.B. 1992. Population regulation in Northern Spotted Owls: theoretical implications for management. In: McCullough, D.; Barrett, R., eds. Wildlife 2001: populations. London: Elsevier: 815-827.

Galeotti, P. 1990. Territorial behavior and habitat selection in an urban population of the Tawny Owl *Strix aluco L.* Bolletino di Zoologia. 57: 59-66.

Hall, P.; Wilson, S.R. 1991. Two guidelines for bootstrap hypothesis testing. Biometrics. 47: 757-762.

Haller, H. 1996. Der Steinadler in Graubünden - langfristige Untersuchungen zur Populationsökologie von *Aquila chrysaetos* im Zentrum der Alpen. Der Ornithologische Beobachter 93: Beiheft. In press.

Hannon, S.; Martin, K. 1996. Mate fidelity and divorce in ptarmigan: polygyny avoidance on the tundra. In: Black, J., ed. Ecology of monogamy: permanent partnerships in birds. Oxford: Oxford University Press: 192-210.

Henny, C.J. 1972. An analysis of the population dynamics of selected avian species with special reference to changes during the modern pesticide era. Wild. Res. Rep. 1. Washington, DC: U.S. Department of Interior. 99 p.

Hirons, G.J.M. 1985. The effects of territorial behavior on the stability and dispersion of Tawny Owl *(Strix aluco)* populations. Journal of Zoology (Series B), London. 1: 21-48.

Houston, C.S. 1987. Nearly synchronous cycles of the Great Horned Owl and snowshoe hare in Saskatchewan. In: Nero, R.W.; Clark, R.J.; Knapton, R.J.; Hamre, R.H., eds. Biology and conservation of northern forest owls: symposium proceedings; 1987 February 3-7; Winnipeg, MB. Gen. Tech. Rep. RM-142. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 56-58.

Houston, C.S.; Francis, C.M. 1995. Survival of Great Horned Owls in relation to the snowshoe hare cycle. Auk. 112: 44-59.

Jenny, D. 1992. Bruterfolg und Bestandsregulation einer alpinen Population des Steinadlers *Aquila chrysaetos*. Der Ornithologische Beobachter. 89: 1-43.

Keith, L.B.; Rusch, D.H. 1989. Predation's role in the cyclic fluctuations of ruffed grouse. Proceedings of the International Ornithological Congress. 19: 699-732.

Kenward, R.E. 1985. Raptor radio-tracking and telemetry. ICBP Technical Publication 5: 409-420.

Kenward, R.E. 1987. Wildlife radio-tagging: equipment, field techniques, and data analysis. London: Academic Press.

Kenward, R.E. 1990. Ranges IV. Wareham, UK: Institute of Terrestrial Ecology, Furzebrook.

Korpimäki, E. 1988. Factors promoting polygyny in European birds of prey - a hypothesis. Oecologia. 77: 278-285.

Korpimäki, E.; Lahti, K.; May, C.A.; Parkin, D.T.; Powell, G.B.; Tolonen, P.; Wetton, J. 1996. Copulatory behavior and paternity determined by DNA fingerprinting in kestrels: effects of cyclic food abundance. Animal Behavior. 51. In press.

Krebs, C.J.; Boutin, S.; Boonstra, R.; Sinclair, A.R.E.; Smith, J.N.M.; Dale, R.T.; Martin, K.; Turkington, R. 1995. Impact of food and predation on the snowshoe hare cycle. Science. 269: 1112-1115.

Lande, R. 1988. Demographic models of the Northern Spotted Owl *(Strix occidentalis caurina)*. Oecologia. 75: 601-607.

Martin, G. 1986. Sensory capacities and the nocturnal habit in owls. Ibis. 128: 266-277.

Martin, G. 1990. Birds by night. London: Poyser.

Matthysen, E. 1989. Territorial and non-territorial settling in juvenile Eurasian nuthatches *(Sitta europaea)* in summer. Auk. 106: 560-567.

McInvaille, W.B.; Keith, L.B. 1974. Predator-prey relations and breeding biology of the Great Horned Owl and Red-tailed Hawk in central Alberta. Canadian Field-Naturalist. 88: 1-20.

Møller, A.P. 1987. Intruders and defenders on avian breeding territories: the effect of sperm competition. Oikos. 48: 47-54.

Nams, V.O. 1990. Locate II. Truro N.S., Canada: Pacer.

Newton, I. 1979. Population ecology of raptors. Berkhamsted: Poyser.

Newton, I. 1991. The role of recruitment in population regulation. Proceedings of the International Ornithological Congress. 20: 1689-1699.

Newton, I. 1992. Experiments on the limitation of bird numbers by territorial behavior. Biological Reviews. 67: 129-173.

Norberg, R.A. 1987. Evolution, structure, and ecology of northern forest owls. In: Nero, R.W.; Clark, R.J.; Knapton, R.J.; Hamre, R.H., eds. Biology and conservation of northern forest owls: symposium proceedings; 1987 February 3-7; Winnipeg, MB. Gen. Tech. Rep. RM-142. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 9-43.

Perrins, C.M. 1991. Constraints on the demographic parameters of bird populations. In: Perrins, C.M.; Lebreton, J.-D.; Hirons, G.J.M., eds. Bird population studies: relevance to conservation and management. Oxford: Oxford University Press: 190-206.

Reynolds, R.T.; Linkhart, B.D. 1990. Extra-pair copulation and extra-range movements in Flammulated Owls. Ornis Scandinavica. 21: 74-77.

Rohner, C. 1995. Great Horned Owls and snowshoe hares: what causes the time lag in the numerical response of predators to cyclic prey? Oikos. 74: 61-68.

Rohner, C. 1996. The numerical response of Great Horned Owls to the snowshoe hare cycle: consequences of non-territorial 'floaters' on demography. Journal of Animal Ecology. 65: 359-370.

Rohner, C. 1997. Non-territorial 'floaters' in Great Horned Owls: space use during a cyclic peak of snowshoe hares. Animal Behaviour. 53: 901-912.

Rohner, C.; Doyle, F.I. 1992. Methods of locating Great Horned Owl nests in the boreal forest. Journal of Raptor Research. 26: 33-35.

Rohner, C.; Hunter, D.B. 1996. First-year survival of Great Horned Owls during a peak and decline of the snowshoe hare cycle. Canadian Journal of Zoology. 74: 1092-1097.

Rohner, C.; Krebs, C.J. 1996. Owl predation on snowshoe hares: consequences of antipredator behavior. Oecologia. 108: 303-310.

Rohner, C.; Krebs, C.J. 1997. Responses of Great Horned Owls to experimental 'hot spots' of snowshoe hare density. Auk. In review.

Rohner, C.; Smith, J.N.M. 1996. Brood size manipulations in Great Horned Owls *Bubo virginianus*: are predators food limited at the peak of prey cycles? Ibis. 138: 236-242.

Rusch, D.H.; Meslow, E.C.; Keith, L.B.; Doerr, P.D. 1972. Response of Great Horned Owl populations to changing prey densities. Journal of Wildlife Management. 36: 282-296.

Saltz, D.; White, G.C. 1990. Comparison of different measures of telemetry error in simulated radio-telemetry locations. Journal of Wildlife Management. 54: 169-174.

Sinclair, A.R.E. 1989. Population regulation in animals. In: Cherrett, J.M., ed. Ecological concepts. Oxford: Blackwell Scientific Publications: 197-241.

Smith, J.N.M.; Arcese, P. 1989. How fit are floaters? Consequences of alternative territorial behaviors in a nonmigratory sparrow. American Naturalist. 133: 830-845.

Smith, S.M. 1978. The "underworld" in a territorial sparrow: adaptive strategy for floaters. American Naturalist. 112: 571-582.

Stamps, J. 1995. Motor learning and the value of familiar space. American Naturalist. 146: 41-58.

Stearns, S.C. 1992. The evolution of life histories. Oxford: Oxford University Press.

Voous, K.H. 1988. Owls of the northern hemisphere. London: Collins Sons.

Watson, A. 1985. Social class, socially-induced loss, recruitment and breeding of red grouse. Oecologia. 67: 493-498.

Watson, A.; Moss, R. 1970. Dominance, spacing behavior and aggression in relation to population limitation in vertebrates. In: Watson, A., ed. Animal populations in relation to their food resources. Oxford: Blackwell Scientific Publications: 167-218.

Weller, M.H. 1965. Bursa regression, gonad cycle and molt of the Great Horned Owl. Bird Banding. 36: 102-112.

Wilcove, D.S.; Terborgh, J.W. 1984. Patterns of population decline in birds. American Birds. 38: 10-13.

Wyllie, I.; Newton, I. 1991. Demography of an increasing population of Sparrowhawks. Journal of Animal Ecology. 60: 749-766.

Monitoring Finnish Owls 1982–1996: Methods and Results

Pertti L. Saurola[1]

Abstract.—In 1982, the *Raptor Grid*, a nation-wide program for monitoring birds of prey was started by the Finnish Ringing Centre. Voluntary banders were asked to select a 10 x 10 km study plot and find annually all active nests or at least occupied territories of birds of prey from their study plot (annual total averaged 120). Since 1986, additional information was collected with the *Raptor Questionnaire.* In 1996, more than 30,000 potential nest sites of owls were checked. The maximum annual number of nests were: e.g., Tengmalm's Owl 2,265, Ural Owl 901, Long-eared Owl 578, Tawny Owl 548, and Eagle Owl 537 nests. During the program, populations remained stable, although the annual fluctuations were extensive. International cooperation is needed to monitor nomadic species.

Efficient monitoring is a vital part of nature conservation in a rapidly changing world. Reliable information on present population status, including size, fecundity, survival and dispersal and annual fluctuations, is necessary to predict long-term trends and to formulate sound management programs. The Northern Spotted Owl (*Strix occidentalis caurina*) is probably the only owl species which has been professionally monitored (e.g., Forsman *et al.* 1996). Unfortunately, in most countries there are insufficient resources to conduct the necessary field work.

In Finland, both the Christmas Bird Count and the Breeding Bird Survey programs (e.g., Koskimies & Väisänen 1991) have produced valuable data for monitoring common land birds. However, these programs do not produce relevant data for monitoring owls. Up to the early 1980s, the only monitoring programs for birds of prey were on the White-tailed Sea Eagle (*Haliaetus albicilla*), Peregrine (*Falco peregrinus*), Golden Eagle (*Aquila chrysaetos*), and Osprey (*Pandion haliaetus*) (Saurola 1985).

The quality of the Finnish amateur ornithologists (ca. 7,000) including, especially, the bird banders (ca. 670) is very high. During the last 20 years, banding of both diurnal and nocturnal birds of prey has had, for several reasons, a high priority (Saurola 1987a). Hence, more than half of the Finnish banders are interested in research and conservation of birds of prey.

In 1982, the Finnish Ringing Centre, with some support for administration from the Ministry of the Environment, started a monitoring project called the *Raptor Grid* to monitor diurnal and nocturnal birds of prey (Saurola 1986). Since 1986, additional information on breeding performance has been collected with the *Raptor Questionnaire* (Haapala & Saurola 1986).

This paper will describe these monitoring techniques based on voluntary work and present some preliminary results on Finnish owl populations during the last 15 years.

MATERIAL AND METHODS

Monitoring Population Size: The *Raptor Grid*

The *Raptor Grid* program is completely based on voluntary field work by raptor banders.

When the project started in 1982, banders were asked (1) to establish a study group consisting of both banders and other bird-watchers, (2) to select a 10 x 10 km study plot, based on "even-ten-kilometers" of the Finnish National Grid, and (3) to try each year to find all the active nests or at least the occupied territories of the diurnal and nocturnal birds of prey in their

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study plot (Saurola 1986). The annual routine for each study plot is: (1) listening for territorial hoots of owls, (2) watching aerial display of buzzards and hawks, (3) searching for nests, (4) listening for fledged broods, and (5) reporting the results in September to the Ringing Centre. In addition, the total number of hours of effort used has to be recorded. For relatively good coverage of all raptor species, about 300–500 person-hours/study plot/breeding season is needed in southern Finland (mixture of boreal forest, agricultural land and lakes). The number of *Raptor Grid* study plots surveyed averaged 120 per year (Haapala *et al.* 1993).

Monitoring Breeding Output: The *Raptor Questionnaire*

In 1982, a Raptor Nest Card was introduced and banders were asked to fill a nest card for birds of prey nests found during the breeding season. The relatively poor response prompted the use of a special summary questionnaire, since 1986, sent to all bird banders. With this simple *Raptor Questionnaire* all banders *must* report a summary of all nests and territories of all birds of prey they have detected during each year.

The *Raptor Questionnaires* summarize the total numbers of (1) potential nest sites checked (table 1), (2) active nests and occupied territories found (table 2), and (3) nests of different clutch and brood sizes verified by banders within the "territories" of 25 local ornithological societies in different parts of the country. Further, the bander has to give information on the amount of field work done by comparing the present and previous seasons according to following scale: the amount of field work on the species was (1) much more than, (2) a little more than, (3) the same as, (4) a little less than, and (5) much less than in the previous season.

The main purpose of the *Raptor Questionnaire* is to collect data on the annual breeding output. In addition, this data, although it cannot be precisely standardized from year to year, may be used with care to detect fluctuations and trends in population sizes, especially when the *Raptor Grid* data is too scanty.

Feed-back articles reporting the results of *Raptor Grid* and *Raptor Questionnaire*-programs have been published every year after the breeding season (e.g., Haapala & Saurola 1986; Haapala *et al.* 1993, 1996).

Monitoring Survival and Dispersal: Banding Programs

For a bander, recaptures and recoveries are the "prize" for the valuable voluntary work described above. Banding is also a basis for monitoring survival and dispersal. In principle, it is fairly simple and straightforward to estimate changes in adult survival from representative long-term capture-recapture data sets (see e.g., Forsman *et al.* 1996). Finnish banders have been encouraged not only to band nestlings but to capture and recapture the adult birds at the nest as well (Saurola 1987a).

Table 1.—*The numbers of potential nest sites of birds of prey checked by Finnish banders in 1996 (excluding the special programs for the eagles, Osprey, and Peregrine).*

Nest sites checked	Number
Big stick nests made by buzzards and hawks	4,579
Small stick nests made by crows and squirrels	2,347
Artificial nests for buzzards and hawks	2,179
Artificial nests for small falcons	4,581
Nest-boxes for the Ural Owl (*Strix uralensis*)	4,583
Nest-boxes for the Tawny Owl (*Strix aluco*)	4,308
Nest-boxes for the Tengmalm's Owl (*Aegolius funereus*)	10,038
Nest-boxes for the Pygmy Owl (*Glaucidium passerinum*)	3,753
Large natural cavities (mainly Black Woodpecker (*Dryocopus martius*) cavities)	2,916
Small woodpecker cavities	3,133
Eagle Owl territories	1,325

Table 2.—*Maximum annual number of active nests, nestlings banded, and adults captured (= banded or recaptured) at the nest of Finnish owls during 1986–1996; the respective record years are given in parenthesis. "Active nest" includes here, in addition to nests found, also broods detected after fledging. The proportion of fledged broods is, however, low except of the "nests" of the Long-eared Owl which may be up to 70 percent. "Population estimate" for non-nomadic species equals the average number of territories occupied annually and for nomadic species (indicated by asterisk) the maximum number of breeding pairs in a peak vole year (Saurola 1985).*

Species	Active nests		Nestlings banded		Adults captured at the nest				Population estimate
					Females		Males		
Eurasian Eagle Owl (*Bubo bubo)*	537	(-94)	803	(-94)	5	(-88)	3	(-89)	2,500
Snowy Owl (*Nyctea scandiaca)*	15	(-88)	20	(-88)	0		0		50 *
Tawny Owl (*Strix aluco)*	548	(-94)	1,535	(-94)	265	(-91)	119	(-94)	2,000
Ural Owl (*Strix uralensis)*	901	(-94)	2,006	(-89)	623	(-94)	72	(-89)	3,000
Great Grey Owl (*Strix nebulosa)*	100	(-89)	200	(-89)	20	(-96)	13	(-96)	1,000 *
Northern Hawk Owl (*Surnia ulula)*	119	(-88)	399	(-89)	10	(-89)	4	(-88)	4,000 *
Eurasian Pygmy Owl (*Glaucidium passerinum)*	274	(-95)	1,005	(-94)	155	(-95)	22	(-91)	2,500
Tengmalm's Owl (*Aegolius funereus)*	2,265	(-89)	6,686	(-89)	1,336	(-89)	191	(-89)	15,000 *
Long-eared Owl (*Asio otus)*	578	(-91)	505	(-88)	2	(-88)	1	(-89)	5,000 *
Short-eared Owl (*Asio flammeus)*	132	(-86)	322	(-88)	5	(-91)	3	(-95)	5,000 *

For owl species breeding in cavities and nest-boxes, the data on adults, especially on females, captured at the nest is fairly extensive, but for open-nesting species they are almost totally missing (table 2).

RESULTS

Some preliminary results from both *Raptor Grid* and *Raptor Questionnaire* are presented. These include for each species (1) a distribution map based on the results of the two Finnish Breeding Bird Atlases (Hyytiä *et al.* 1983, Väisänen unpubl. data; figs. 1, 4–12), (2) a column chart for the entire country and corresponding charts for the areas of all local ornithological societies showing the annual numbers of nests and territories found by banders (figs. 1, 4–12), and (3) a diagram of average annual production of young per active nest (excluding the Snowy Owl) in 1986–1996 (fig. 3). In addition, (4) the annual population indices derived from the *Raptor Grid* data are shown for five well-covered species (fig. 2). Please note that all these figures are based on raw data, which has not been corrected with the information on possible changes in the amount and quality of field-work carried out. However, the essential effects of changing effort have been mentioned in the text.

Eurasian Eagle Owl

In the early 1960s, the Eurasian Eagle Owl (*Bubo bubo bubo* (L.)) was not protected by law and it was considered, by conservationists, an endangered species in Finland. Protection during the breeding season was finally given in 1966 and since 1983 the Eagle Owl has been protected year round. In addition to full protection, clearcutting of forests, and stable anthropogenic food resources, i.e., large Norwegian rat (*Rattus norvegicus*) populations at rubbish dumps, have been the most important causes of the rapid recovery of the population (Saurola 1985). The Eagle Owl now breeds all over Finland except the northernmost tundra, with highest density in the west–southwest (fig. 1). Since 1982, the population has been slowly increasing (fig. 2). The effect of fluctuating vole populations can be clearly observed in the number of breeding attempts (figs. 1–2), but is not as evident in the breeding output of those pairs which have started to breed (fig. 3).

It is important to predict the population trend of this controversial species. For that purpose it is necessary to have relevant capture-recapture data for survival and dispersal analyses. In total, more than 5,580 nestlings have been ringed during the last 10 years, but only very

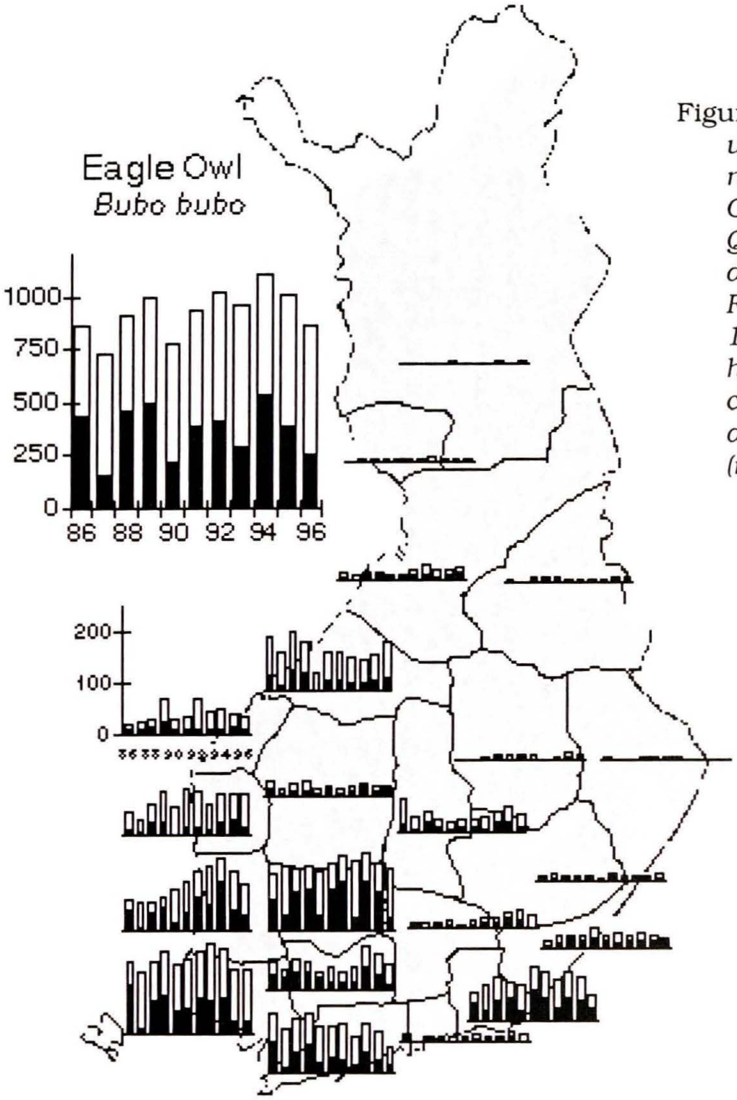

Figure 1.—*Number of active nests (black columns) and occupied territories, where no nest was found (white columns) of the Eagle Owl (*Bubo bubo*) based on the Raptor Questionnaire in 1986–1996. The breeding distribution (shaded area) is based on the Finnish Breeding Bird Atlases (Hyytiä* et al. *1983 and Väisänen unpubl. data). The large histograms include data from the entire country; small histograms show data by the areas of the local ornithological societies (note different scales).*

few adults have been captured at the nest (e.g., table 2). The Eagle Owl is a very shy breeder. So far, attempts to develop an efficient, but safe method to catch adults at nests have not succeeded.

Snowy Owl

The nomadic Snowy Owl (*Nyctea scandiaca* (L.)) is only an occasional breeding bird in Finland. Only when a Snowy Owl invasion from the east coincides with a microtine peak will breeding occur in the northernmost highlands and bogs of Finnish Lapland (fig. 4). This most recently occurred in 1988, 1987, and 1974. Before 1974, no observations of breeding Snowy Owls were made for several decades in Finland. A few individuals have been seen every winter, especially in the southwestern archipelago, but mass winter invasions seldom occur, the last being the two successive winters of 1960–1961 and 1961–1962.

Tawny Owl

The Tawny Owl (*Strix aluco aluco* L.) is a newcomer to Finland from Middle Europe: the first observation was made in 1875 and the first breeding attempt was verified in 1878 (e.g., Saurola 1995). It has the most southerly distribution of all Finnish owl species (fig. 5). Because the Tawny Owl is a year-round resident, the northern boundary of its distribution is most probably determined by winter mortality. For instance, during the harsh winter 1986–1987 a big proportion of the population starved to death. The population recovered rapidly, but again suffered high mortality

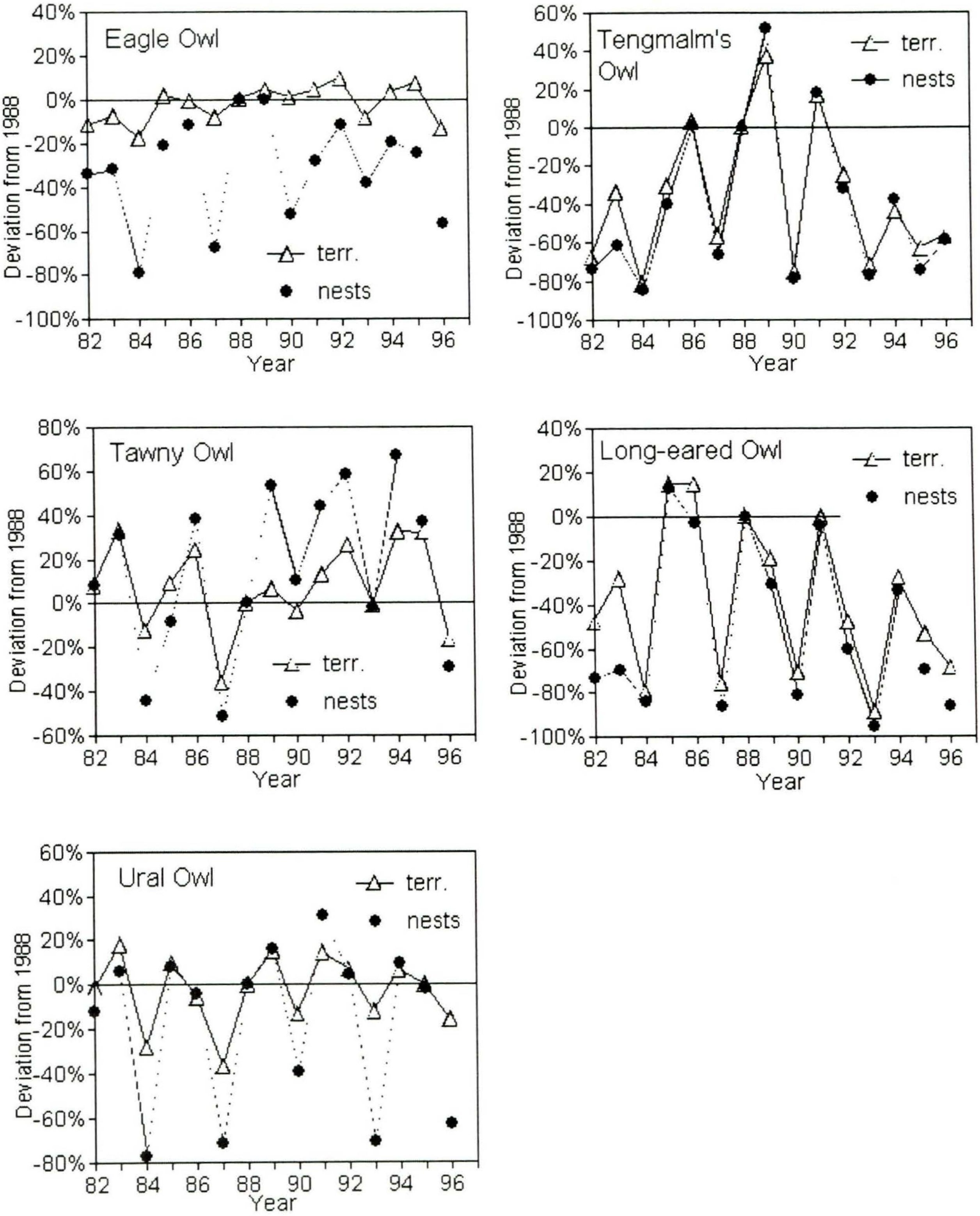

Figure 2.—*Annual variation of the population indices of the Eagle Owl (*Bubo bubo*), Tawny Owl (*Strix aluco*), Ural Owl (*Strix uralensis*), Tengmalm's Owl (*Aegolius funereus*), and Long-eared Owl (*Asio otus*) in Finland, based on data from the Raptor Grid program in 1982–1996. The indices were calculated as percentual deviations from the reference year 1988. Dots = active nests, triangles= all occupied territories (including active nests).*

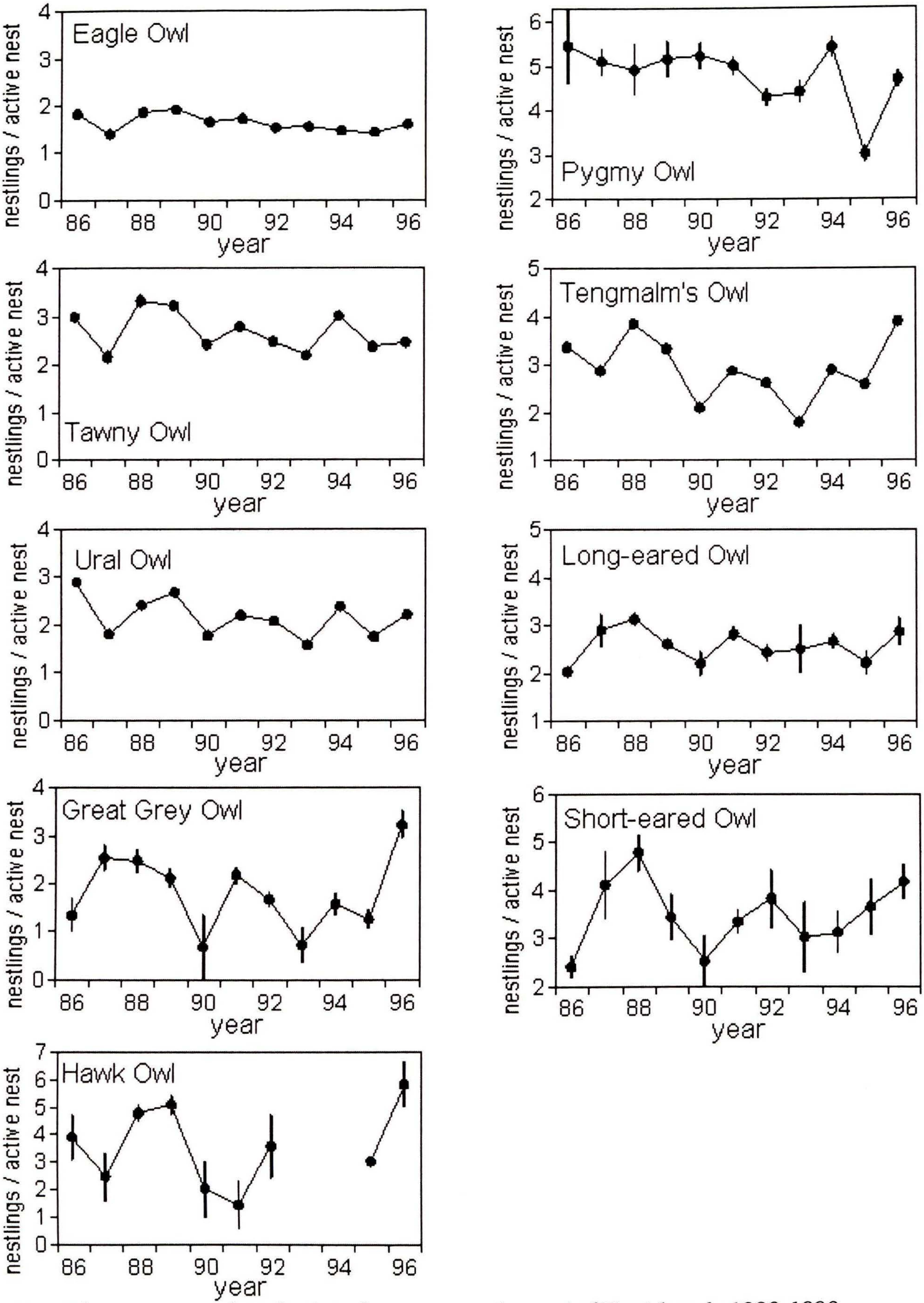

Figure 3.—*The mean annual production of young per active nest of Finnish owls 1986–1996. Standard errors indicated by vertical lines.*

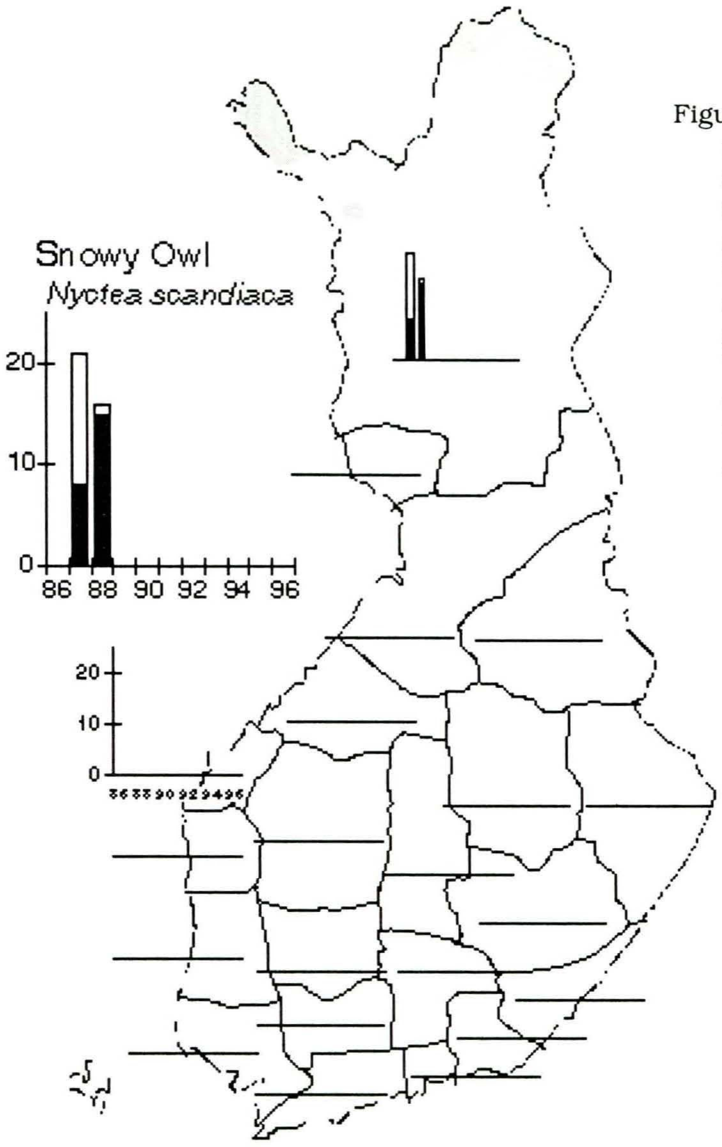

Figure 4.—*Number of active nests (black columns) and occupied territories, where no nest was found (white columns) of the Snowy Owl (*Nyctea scandiaca*) based on the Raptor Questionnaire in 1986–1996. The breeding distribution (shaded area) is based on the Finnish Breeding Bird Atlases (Hyytiä* et al. *1983 and Väisänen, unpubl. data). The large histograms include data from the entire country; small histograms show data by the areas of the local ornithological societies (note different scales).*

during the winter 1995–1996 (unpubl. data, fig. 2). The Tawny Owl is a generalist feeder relative to other Finnish owls, but good and bad vole years clearly affect its breeding performance (Linkola and Myllymäki 1969, figs. 2-3, 5).

The population ecology of the Tawny Owl has been studied for more than 30 years, but few results have been published so far (e.g., Linkola and Myllymäki 1969, Saurola 1987b). In the best year, more than 1,500 nestlings were banded and almost 400 adults captured at the nest (table 2). The first attempts to estimate the annual variation in survival both by using recoveries of birds found dead (Rinne *et al.* 1990, 1993) and recaptures of breeding birds (Saurola, unpubl. data) have already been made.

Ural Owl

The Ural Owl (*Strix uralensis liturata* Lindr.) breeds in coniferous and mixed forests all over Finland up to the southern part of Lapland (fig. 6). However, along the southern and western coastal areas the population is sparse, probably because of competition with and predation by the Eagle Owl. Further, the population density is also very low in northern Finland, where the Ural Owl is mainly replaced by the Great Gray Owl, which is more invasive and better adapted to catch voles through thick snow. In contrast, low numbers of nests found in southeastern Finland are partly due to the lower bander activity.

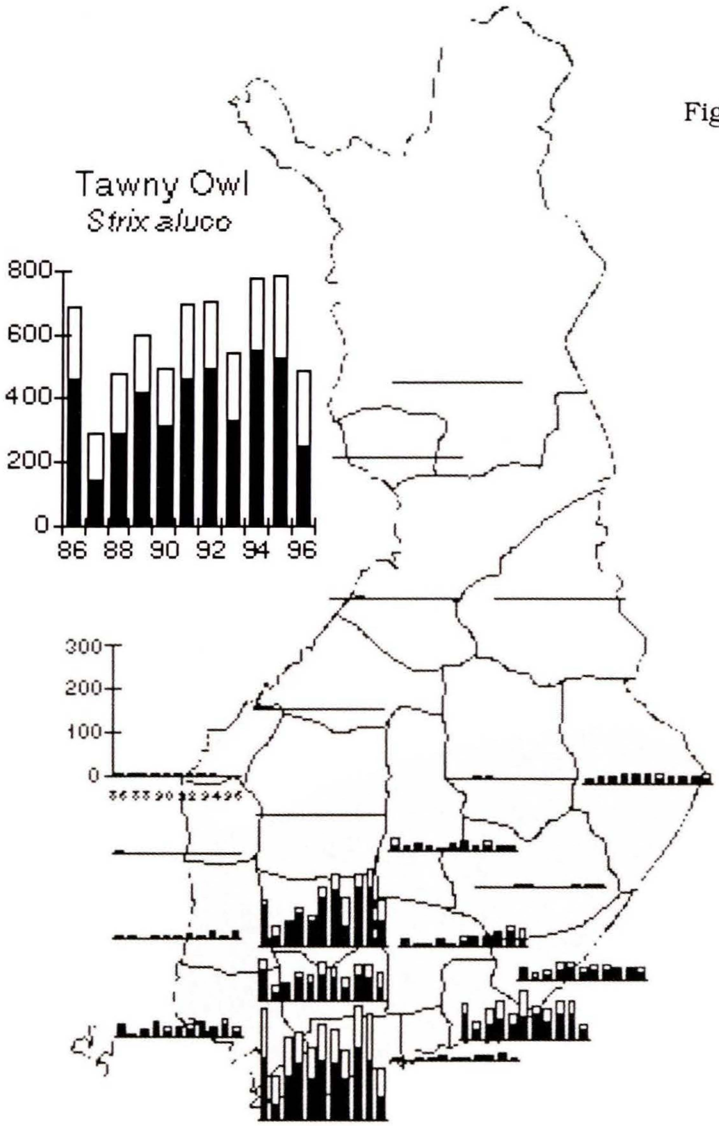

Figure 5.—*Number of active nests (black columns) and occupied territories, where no nest was found (white columns) of the Tawny Owl (*Strix aluco*) based on the Raptor Questionnaire in 1986–1996. The breeding distribution (shaded area) is based on the Finnish Breeding Bird Atlases (Hyytiä* et al. *1983 and Väisänen, unpubl. data). The large histograms include data from the entire country; small histograms show data by the areas of the local ornithological societies (note different scales).*

The population ecology of the Ural Owl have been studied intensively during the last 30 years in two areas in Finland (e.g., Linkola and Myllymäki 1969; Pietiäinen 1989; Pietiäinen and Kolunen 1993; Saurola 1989, 1992). These studies have shown that the breeding performance of the Ural Owl is strongly dependent on fluctuating vole populations. This also can be clearly seen in figures 2, 3, and 6: both the number of breeding attempts and the production of young per attempt have followed a pattern determined by voles. The total number of active nests found in good vole years (fig. 6) seems to have increased slightly during the last 10 years, but more standardized data (Saurola 1992 and unpubl., fig. 2,) does not show any kind of trend during the 1970s, 1980s, and 1990s.

High numbers of nestlings have been banded and females captured (banded/recaptured) at the nest during the last 20 years (table 2), but the analysis on survival rates is not yet finished (Saurola, in prep.). Both recaptures and recoveries of dead birds have shown that the nest site fidelity of breeding Ural and Tawny Owls is very high (Saurola 1987b), which means that figures 2 and 6 reflect actual fluctuations in Finnish populations of these species.

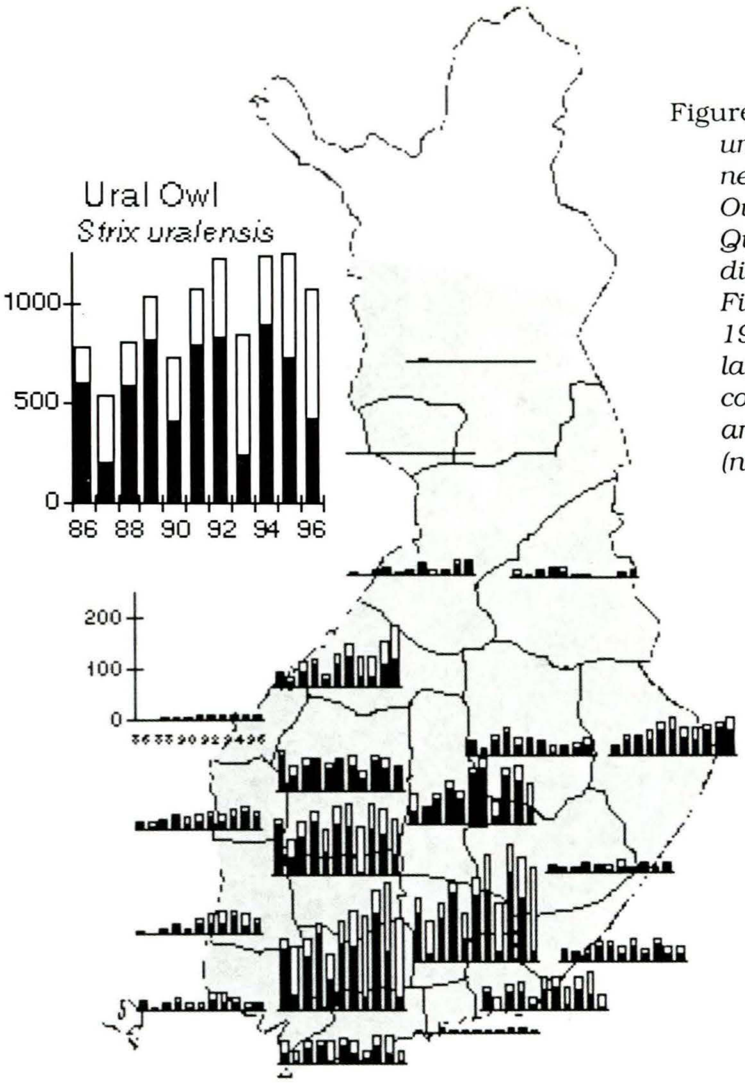

Figure 6.—*Number of active nests (black columns) and occupied territories, where no nest was found (white columns) of the Ural Owl (*Strix uralensis*) based on the Raptor Questionnaire in 1986–1996. The breeding distribution (shaded area) is based on the Finnish Breeding Bird Atlases (Hyytiä* et al. *1983 and Väisänen, unpubl. data). The large histograms include data from the entire country; small histograms show data by the areas of the local ornithological societies (note different scales).*

Great Gray Owl

In principle, a breeding pair of the Great Gray Owl (*Strix nebulosa lapponica* Thunb.) may be found anywhere in Finland, except in the southwestern archipelago and the northwestern corner of Lapland (fig. 7). However, in practice, the Great Gray Owl is a very rare breeder in the southern third of the country (cf. the Ural Owl, fig. 6). Since the late 1960s, the number of active nests found have increased considerably. Although a part of the increase may be attributed to the increased activity of banders and other bird-watchers in northern Finland, the Finnish Great Gray Owl population has certainly increased from the very low level in the 1940s, 1950s, and early 1960s (Sulkava 1997). Compared with the two hole-nesting *Strix*-species, the Great Gray Owl has been studied very little in Finland (cf. table 2). A few band recoveries suggest that a (small) part of the Finnish population is resident, while the others are nomadic.

Northern Hawk Owl

The potential breeding distribution of the Northern Hawk Owl (*Surnia ulula ulula* (L.)) extends all over Finland. However, during the last decades its distribution has been restricted to the northern half of the country (fig. 8). The hawk owl is a nomad which follows vole peaks across wide areas in northern forests: e.g., two nestlings banded in Finland were encountered

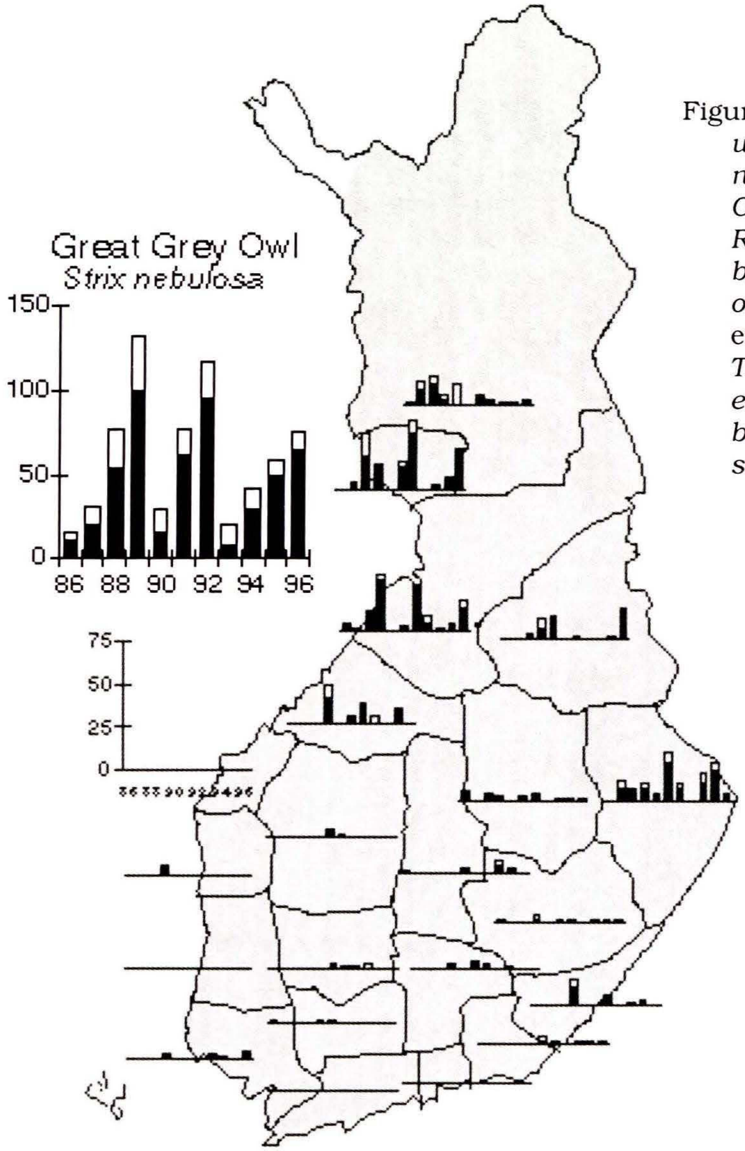

Figure 7.—*Number of active nests (black columns) and occupied territories, where no nest was found (white columns) of the Great Gray Owl (*Strix nebulosa*) based on the Raptor Questionnaire in 1986–1996. The breeding distribution (shaded area) is based on the Finnish Breeding Bird Atlases (Hyytiä* et al. *1983 and Väisänen, unpubl. data). The large histograms include data from the entire country; small histograms show data by the areas of the local ornithological societies (note different scales).*

east of the Ural mountains, 2,700 km away, and three others from southern Norway, 1,200–1,400 km away from their natal areas (Saurola 1995). Thus, the hawk owl is a very difficult species to study and monitor. Banding totals indicate that during the last 3 decades 1–2 year peaks in breeding (1974, 1977–1978, 1982–1983, and 1988–1989) have followed each other with 3–5 year intervals. However, after the last peak year, breeding hawk owls have been almost absent from Finland for 7 years (fig. 8).

Eurasian Pygmy Owl

The Eurasian Pygmy Owl (*Glaucidium passerinum passerinum* (L.)) extends its distribution from the southern coast to middle part of Lapland (fig. 9). Ten years ago the Pygmy Owl was included in the Red Data Book of Finland and the population estimate (= "academic guess") was 2,500 pairs (table 2, Saurola 1985). Since then new information has been gathered as a result of the development of special thick-front-wall nest boxes and early morning hoot excursions. The Pygmy Owl is no longer included in the Red Data Book and the population "guesstimate" should be 3–4 times higher. At the moment, no population trend can be derived from the data (fig. 9), because it reflects the high correlation between the number of available nest boxes and the number of nests found (r = 0.87).

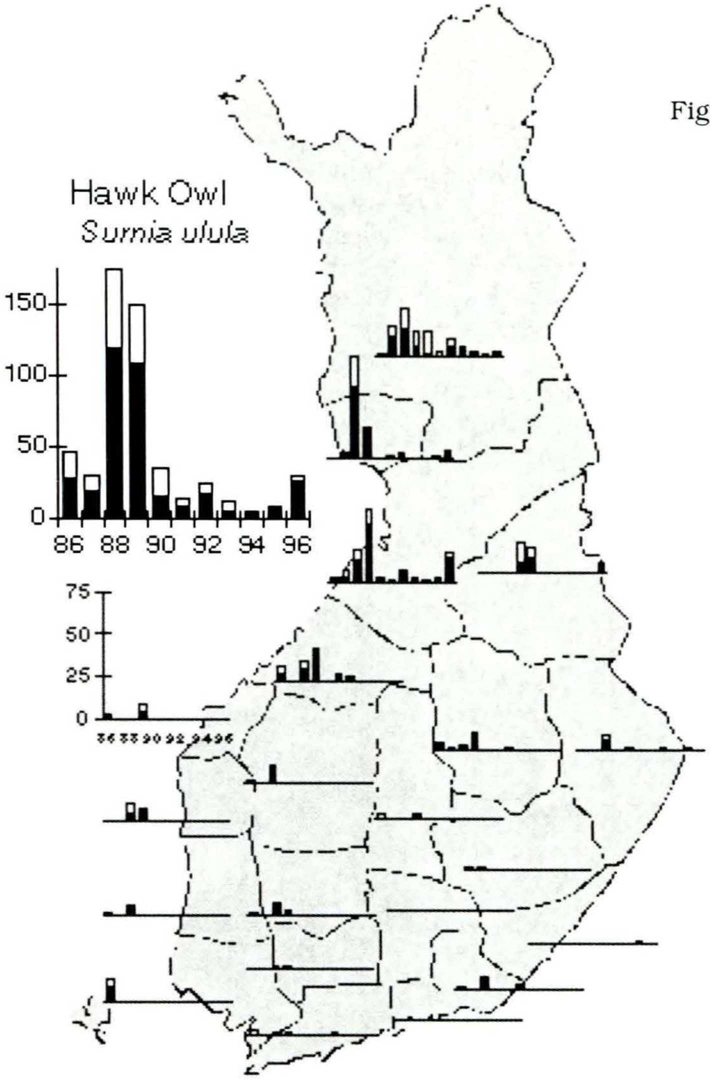

Figure 8.—*Number of active nests (black columns) and occupied territories, where no nest was found (white columns) of the Hawk Owl (*Surnia ulula*) based on the Raptor Questionnaire in 1986–1996. The breeding distribution (shaded area) is based on the Finnish Breeding Bird Atlases (Hyytiä* et al. *1983 and Väisänen, unpubl. data). The large histograms include data from the entire country; small histograms show data by the areas of the local ornithological societies (note different scales).*

Tengmalm's Owl

The Tengmalm's Owl (*Aegolius funereus funereus* (L.)) breeds in various kinds of forests and woodlands all over Finland, from the southern archipelago to northernmost Lapland (fig. 10). It is the most common and abundant of the Finnish owls. It is also the most intensively and extensively studied owl species in Finland (e.g., Korpimäki 1981, 1992a; Korpimäki and Hakkarainen 1991; Korpimäki and Lagerström 1988). Figures 2 and 10 indicate that the breeding population of the Tengmalm's Owl has fluctuated with a 3-year pattern, in fairly extensive synchrony over large areas in southern Finland, and in rhythm with other owl species. The Tengmalm's Owl had an exceptionally good year in 1989 especially along the central part of the west coast. This was probably due both to the high breeding output in 1988 and the exceptionally strong immigration of Tengmalm's Owls to the west coast in 1989. Band recoveries suggest that Finnish Tengmalm's Owls are partly nomadic: when the vole populations crash, females emigrate but males try to survive on their territories (Korpimäki *et al.* 1987).

Long-eared Owl

The Long-eared Owl (*Asio otus otus* (L.)) breeds in various kinds of woodlands, often close to agricultural areas, from the southern coast to southern Lapland (fig. 11). The Long-eared Owl is a vole specialist, which breeds only when *Microtus* populations are high (Korpimäki

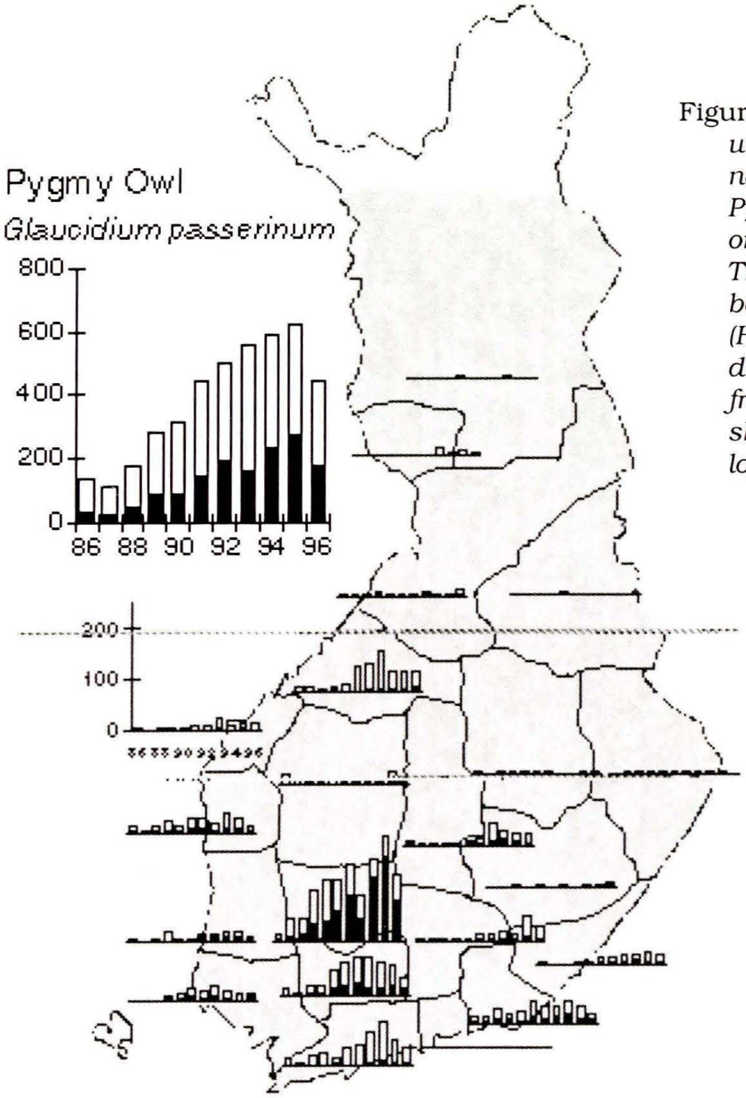

Figure 9.—*Number of active nests (black columns) and occupied territories, where no nest was found (white columns) of the Pygmy Owl* (Glaucidium passerinum) *based on the Raptor Questionnaire in 1986–1996. The breeding distribution (shaded area) is based on the Finnish Breeding Bird Atlases (Hyytiä* et al. *1983 and Väisänen, unpubl. data). The large histograms include data from the entire country; small histograms show data by the areas of the local ornithological societies (note different scales).*

1992b). In Finland it is migratory and at least partly or perhaps totally nomadic (Saurola 1983). Both the number of active nests and occupied territories have fluctuated widely with a 3-year pattern across most of southern Finland (figs. 2 and 11). Since 1986, the total number of nests found in peak years in Finland has been stable, except in 1995, when voles crashed in early spring (fig. 11). Because many of the Long-eared Owl nests have been found after the young start to beg, the bander's data on the reproductive output is biased: the average number of young produced per active nest is likely too high, but probably comparable over the years (fig. 3).

Short-eared Owl

The Short-eared Owl (*Asio flammeus flammeus* (Pont.)) may breed all over Finland from the southern archipelago to northernmost Lapland (fig. 12). However, as figure 12 indicates, there are very few breeding records since 1986 in the southern part of the country. The Short-eared Owl is migratory and mostly, if not totally, nomadic (Korpimäki 1992b, Saurola 1983). Because Short-eared Owls are active and conspicuous during the day, occupied territories are easily detected. In contrast, much more work and motivation is needed for finding the well-hidden nest in a marsh, meadow, or field. This difference can be observed in figure 12: from some areas only territories are reported.

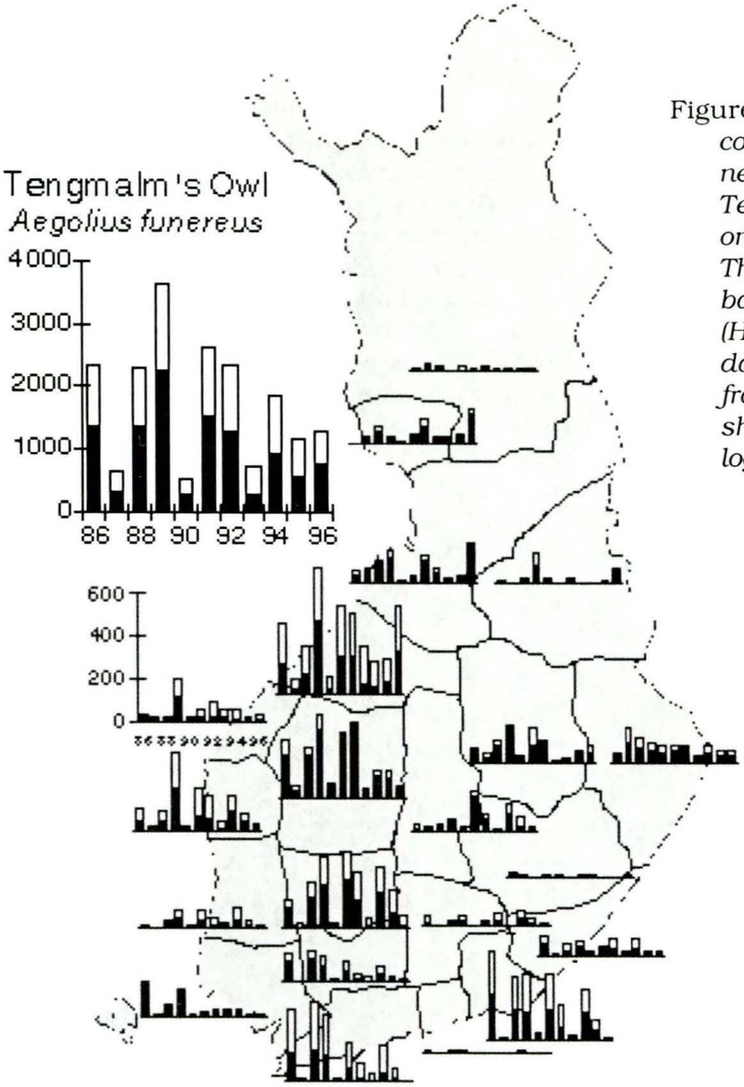

Figure 10.—*Number of active nests (black columns) and occupied territories, where no nest was found (white columns) of the Tengmalm's Owl* (Aegolius funereus) *based on the Raptor Questionnaire in 1986–1996. The breeding distribution (shaded area) is based on the Finnish Breeding Bird Atlases (Hyytiä* et al. *1983 and Väisänen, unpubl. data). The large histograms include data from the entire country; small histograms show data by the areas of the local ornithological societies (note different scales).*

DISCUSSION

Methodological Biases

Raptor Grid

Incomplete Coverage.—This sampling method is, in principle, very simple, but in practice for some species very laborious, when the study plot is 100 km^2. Hence, the variation in search effort and success is high between the study plots. Because the aim of this project is to produce annual population indices for detecting long-term trends, variation between study plots is not critical, providing that effort from year to year within each study plot remains the same.

Turnover of Study Plots.—In principle, the set of study plots and the search effort in each study plot should be the same from year to year. In practice, because the work is voluntary, some study plots become inactive and new ones emerge (Haapala *et al.* 1993). However, this bias may be mitigated by using an appropriate statistical procedure when analyzing the data. Here (fig. 2) all years were compared pairwise with the reference year 1988, which was in general a good year with much data and fairly close to the middle of the study period. This very simple method is relatively unbiased. However, quite a large amount of data from study plots which were not active in 1988 was not used, and, in the future, more sophisticated analytical methods should be used.

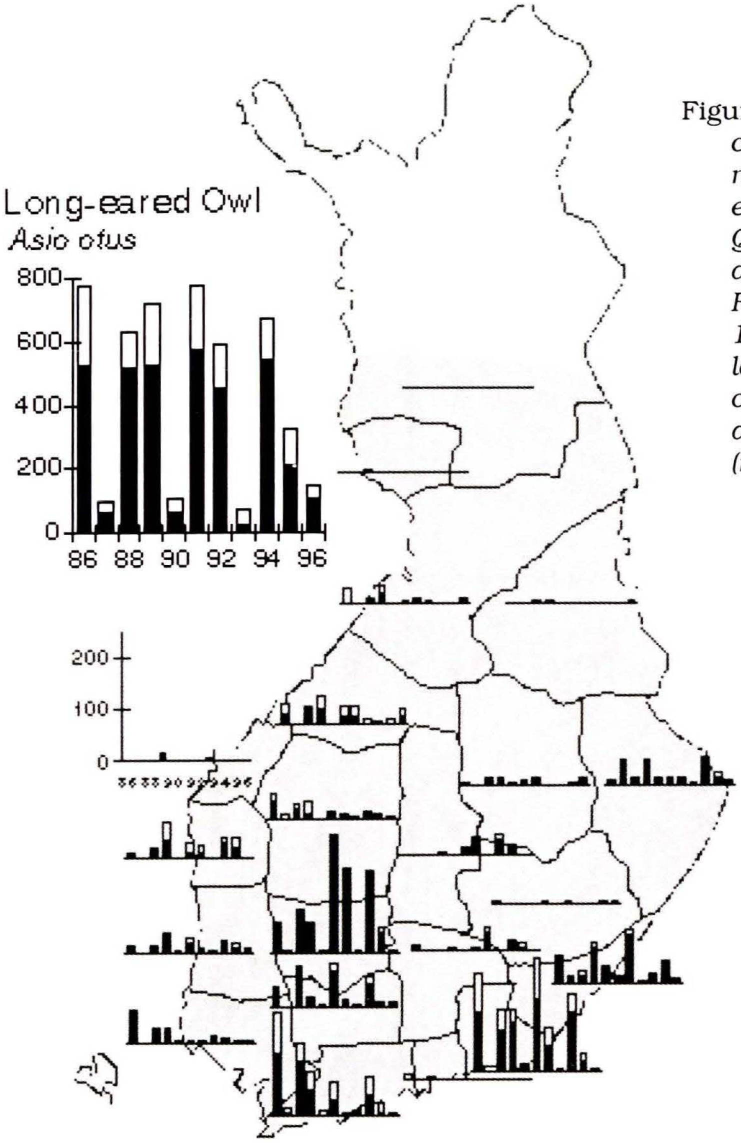

Figure 11.—*Number of active nests (black columns) and occupied territories, where no nest was found (white columns) of the Long-eared Owl* (Asio otus) *based on the Raptor Questionnaire in 1986–1996. The breeding distribution (shaded area) is based on the Finnish Breeding Bird Atlases (Hyytiä* et al. *1983 and Väisänen, unpubl. data). The large histograms include data from the entire country; small histograms show data by the areas of the local ornithological societies (note different scales).*

Semi-random Selection of Study Plots.—Because the *Raptor Grid* 10 x 10 km study plots have not been selected randomly, they may be better areas for birds of prey than other potential study plots nearby, and, hence, the changes detected may not represent the changes in the entire population. Although the banders may freely select their study plots, the boundaries ("even-ten-kilometer" lines) of the plots are randomly pre-determined by the National Grid. For this reason, the quality differences between such large plots and other potential plots nearby are small.

Geographical Distribution of *Raptor Grid* Study Plots.—The number of resident banders is very low in northern Finland and, consequently, the data from both the *Raptor Grid* and the *Raptor Quetionnaire* is not representative for the northern half of the country. This bias is very difficult to avoid without extra funding for travel costs for visiting banders from southern Finland.

Raptor Questionnaire

Population Changes.—The total amount of annual field work done by banders in searching for nests is not constant, although most of the banders have a traditional banding "territory" where they check the same nest-boxes and territories from year to year. So far, the total effort has been increasing: new permits for raptor banders have been issued and some of the veteran banders have increased their effort, e.g., by putting up more nest boxes within their

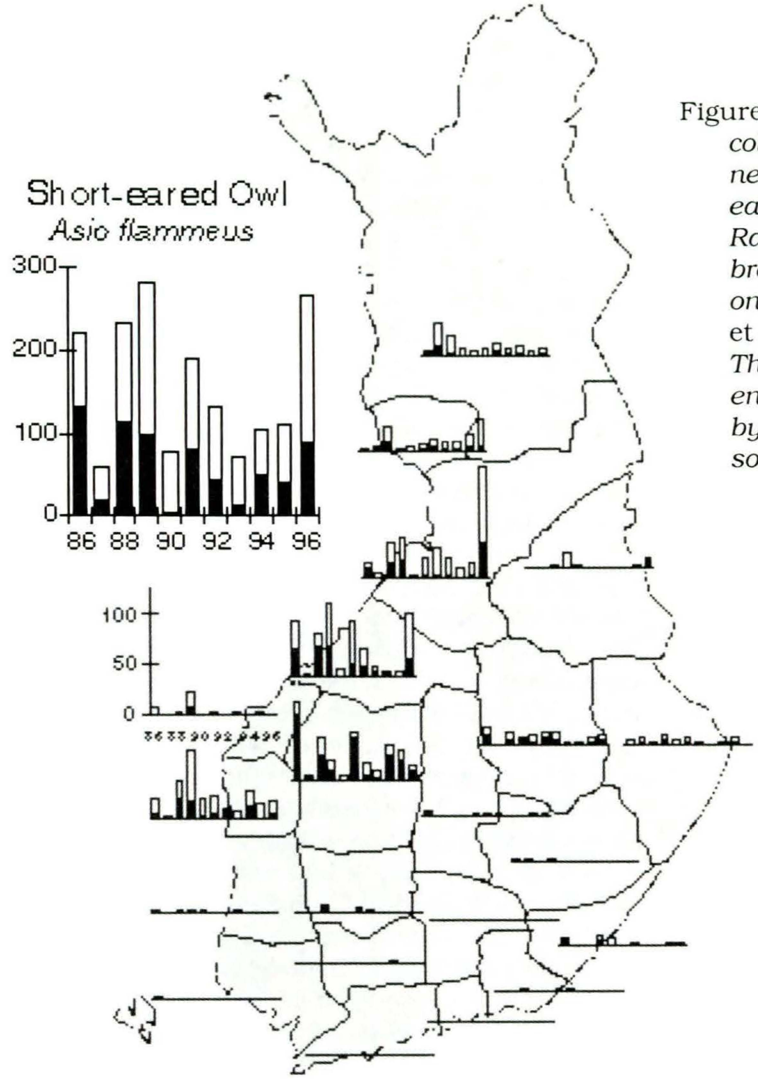

Figure 12.—*Number of active nests (black columns) and occupied territories, where no nest was found (white columns) of the Short-eared Owl (*Asio flammeus*) based on the Raptor Questionnaire in 1986–1996. The breeding distribution (shaded area) is based on the Finnish Breeding Bird Atlases (Hyytiä* et al. *1983 and Väisänen, unpubl. data). The large histograms include data from the entire country; small histograms show data by the areas of the local ornithological societies (note different scales).*

banding territory. In principle, the data could be corrected for the change in effort (see MATERIAL AND METHODS), but this was not done.

Breeding Output.—Data from the *Raptor Questionnaire* gives a fairly reliable picture of the annual breeding output of Finnish owls. However, two potential biases must be noted. First, a successful nest of an open-nesting species is probably found more often than an unsuccessful one. Thus, the breeding output of some open-nesting species (e.g., the Long-eared Owl) may be too high (fig 3). Second, the breeding output in nest boxes may not represent the entire population.

Nest boxes vs. Natural Cavities

Nest box programs were started as a conservation measure to compensate for the loss of natural owl nest sites by commercial forestry. Later, the use of nest boxes became a research method to find and reach owl nests much more easily than in natural circumstances. However, some potential biases must be taken into account when analyzing data from nest box programs.

Population Changes.—If only a small part of the population breeds in nest boxes, and if the number of natural nest sites becomes an important limiting factor, a decrease of the "natural population" will not be detected if all data comes from the "nest box population".

There should still be enough woodpecker cavities available for the Pygmy Owl almost everywhere in Finland. In contrast, commercial forests which are exploited intensively without a positive attitude for conservation, may lack sufficient Black Woodpecker (*Dryocopus martius*) cavities for the Tengmalm's Owl. The Tawny Owl breeds in association with human settlements and may use, in addition to Black Woodpecker cavities and nest boxes for owls, other suitable man-made nest sites like buildings and vacant nest-boxes constructed for the Goldeneye (*Bucephala clangula*) and Goosander (*Mergus merganser*). The Ural Owl probably suffers more than any other Finnish owl species from the lack of good natural nest sites: large cavities in big trees and chimney-like stumps, which are very rare in modern forests. The Ural Owl may nest in vacant hawk nests, although it is not well-adapted to breed in stick nests (see below).

Breeding output.—Properly constructed and placed nest boxes may be better nest sites than natural ones. In virgin forests the number of nest sites is probably large enough that the difference between nest boxes and natural sites accepted by owls is negligible. In commercial forests, in contrast, nest boxes may be, on average, more productive nest sites than natural ones. If so, the data on breeding output from nest box studies does not represent "normal" reproductive success in commercial forests. For example, Ural Owl females may, by scraping the nest bowl deeper and deeper during incubation, push the eggs down through the bottom of a thin stick nest. This cannot happen in a cavity or in a nest box. In addition, young leave a stick nest sooner and are more vulnerable to predators than those in a deep cavity, stump, or nest box.

Evaluation and Potential Improvements

Resident Species

Population Size and Breeding Output.—In principle, it is an easy and straightforward task to monitor resident species. Thus, alarming changes both in population size and breeding output of the Eagle Owl, Tawny Owl, and Ural Owl should be detected by the present monitoring system. Data for the Pygmy Owl comes from a short period and from a fairly restricted area and, hence, the value of any conclusions is so far quite restricted. But "Pygmy Owl disease" is quickly spreading among the banders and within some years the Pygmy Owl will probably be among the well-monitored species as well.

The Finnish Tengmalm's Owl is intermediate between a resident and a nomad: males stay but females emigrate hundreds of kilometers. Thus, local long-term population studies are partly based on resident males (e.g., Korpimäki 1992a). However, the existing banding results suggest, that in contrast to the "real" nomadic species (see below), we may speak about the "Finnish population" of the Tengmalm's Owl. So, the present monitoring system should produce representative data on this intermediate species, too.

Survival.—Monitoring changes in adult and juvenile survival is much more complicated but is at least as important as monitoring fecundity. There is an extensive capture-recapture data set for Ural Owl females caught at the nest and fairly good data on the Tawny Owl; but data on male Ural Owls is, in practice, restricted to my own study area. An analysis of these data is under preparation (Saurola in prep.). Female Tengmalm's Owls have been caught as efficiently as females of the two nest-box using *Strix*-species, from 50–60 percent of known nests, but the proportion of recaptures has been much lower (15–20 percent vs. 70–80 percent in *Strix*). Because of female nomadism this data cannot easily be used for survival analysis. Data on male Tengmalm's Owls comes mainly from Erkki Korpimäki's study area (Korpimäki 1992a).

Survival during the first year of life cannot be estimated with the capture-recapture method. Estimates based only on recoveries of birds banded as nestlings and found dead by the general public are unreliable. However, there is still some methodological work going on, especially analyzing the Finnish Tawny Owl and Ural Owl recoveries (Rinne *et al.* 1990, 1993, and in prep.).

Nomadic Species

In fact, there are no resident "Finnish breeding populations" of the Snowy Owl, Northern Hawk Owl, and Great Gray Owl. These "populations" are only individuals of a large nomadic population from northern Russia through Finland and Sweden to Norway which happen to breed now and then in Finland. The Short-eared Owl belongs to the same group, but the common area of its "Western-Palearctic population" extends much further south. Long-eared Owls breeding in Finland are also nomads, but probably on a much smaller scale (perhaps mainly within Finland ?). These conclusions are based mostly on "common sense" and not on hard data: there are very few band recoveries of dead birds and hardly any recaptures at nests showing the real extent of the breeding and natal dispersal of these species.

It is not possible to monitor nomadic species properly without intensive cooperation over large areas in northern Europe and across national boundaries. At least during the peak years for these species, which are easily detected, extra study plots should be established to estimate their densities, nestlings should be banded, and the adults banded/recaptured at nests as extensively as possible in all countries sharing the populations. These proposals are of course impossible to realize all over northern Russia. But for the Nordic countries, and perhaps including northwestern Russia, a joint "Nomadic Owls" program is perhaps not unrealistic if the idea is properly "sold" to volunteers.

CONCLUDING REMARKS

1. In Finland, good cooperation between professional-level volunteers (bird banders) and organizations responsible for monitoring bird populations (Ministry of Environment and the Finnish Museum of Natural History) has produced valuable data for monitoring diurnal and nocturnal birds of prey. In fact, for economical reasons, this has been the only way to get such important information.

2. The data available does not suggest any alarming negative trends during the last 15 years for any resident species of Finnish owls.

3. However, in many areas in Finland, commercial forests have been heavily harvested and hole-nesting owl species suffer from the lack of natural nest sites: suitable cavities in hollow trees. In those areas, hole-nesting owls are dependent on the continuous voluntary work of owl banders, who try to compensate the losses with appropriate nest-boxes.

4. More fieldwork and international cooperation is needed before reliable conclusions on nomadic species are possible.

ACKNOWLEDGMENT

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LITERATURE CITED

Forsman, E.D.; DeStefano, S.; Raphael, M.G.; Gutiérrez, R.J., eds. 1996. Demography of the Northern Spotted Owl. Studies in Avian Biology No. 17. Cooper Ornithological Society. 120 p.

Haapala, J.; Saurola, P. 1986. Breeding of raptors and owls in Finland in 1986 (in Finnish with English summary). Lintumies. 21: 258–267.

Haapala, J.; Lehtonen, J.T.; Korhonen, J.; Saurola, P. 1993. Breeding and population trends of common raptors and owls in Finland in 1992 (in Finnish with English summary). Linnut. 28 (1): 18–27.

Haapala, J.; Korhonen, J.; Saurola, P.. 1996. Breeding and population trends of common raptors and owls in Finland in 1995 (in Finnish with English summary). Hippiäinen. 26(2): 4-11.

Hyytiä, K. Kellomäki, E.; Koistinen, J. 1983. Suomen lintuatlas. SLY:n Lintutieto Oy. Helsinki. Finland. 520 p.

Korpimäki, E. 1981. On the ecology and biology of Tengmalm's Owl (*Aegolius funereus*) in Southern Ostrobothnia and Suomenselkä western Finland. Acta Universitatis Ouluensis. Series A. Scientiae Rerum Naturalium. 118: 1–84.

Korpimäki, E. 1992a. Fluctuating food abundance determines the lifetime reproductive success of male Tengmalm's Owls. Journal of Animal Ecology. 61: 103–111.

Korpimäki, E. 1992b. Population dynamics of Fennoscandian owls in relation to wintering conditions and between-year fluctuations of food. In: Galbraith, C.A.; Taylor, I.; Percival, S., eds. The ecology and conservation of European owls. UK Nature Conserv. 5. Peterborough, Great Britain: Joint Nature Conservation Committee: 1–10.

Korpimäki, E. Hakkarainen, H. 1991. Fluctuating food supply affects the clutch size of Tengmalm's Owl independent of laying date. Oecologia. 85: 543–552.

Korpimäki, Erkki; Lagerström, M. 1988. Survival and natal dispersal of fledglings of Tengmalm's Owl in relation to fluctuating food conditions and hatching date. Journal of Animal Ecology. 57: 433–441.

Korpimäki, E.; Lagerström, Martti; Saurola, Pertti. 1987. Field evidence for nomadism in Tengmalm's Owl *Aegolius funereus*. Ornis Scandinavica. 18: 1–4.

Koskimies, P.; Väisänen, R.A. 1991. Monitoring bird populations: a manual of methods applied in Finland. Finnish Museum of Natural History. 144 p.

Linkola, P.; Myllymäki, A. 1969. Der Einfluss der Kleinsäugerfluktuationen auf das Brüten einiger Kleinsäugerfressenden Vögel im südlichen Häme, Mittelfinnland 1952–66. Ornis Fennica. 46: 45–78.

Pietiäinen, H. 1989. Seasonal and individual production of offspring in the Ural Owl *Strix uralensis*. Journal of Animal Ecology. 58: 905–920.

Pietiäinen, H.; Kolunen H. 1993. Female body condition and breeding of the Ural Owl *Strix uralensis*. Functional Ecology. 7: 726–735.

Rinne, J.; Lokki, H.; Saurola, P. 1990. Survival estimates of nestling recoveries: forbidden fruits of ringing? Ring. 13: 255–270.

Rinne, J.; Lokki, H.; Saurola, P. 1993. Extensive parametrisation of survival models for recovery data analysis. In: Lebreton, Jean-Dominique; North, Philip M., eds. Marked individuals in the study of bird populations. Birkhäuser Verlag. Basel. Switzerland: 65–75.

Saurola, P. 1983. Movements of Short-eared Owls (*Asio flammeus*) and Long-eared Owls (*Asio otus*) according to Finnish ring recoveries (in Finnish with English summary). Lintumies. 18: 67–71.

Saurola, P. 1985. Finnish birds of prey: status and population changes. Ornis Fennica. 62: 64–72.

Saurola, P. 1986. The *Raptor Grid*: an attempt to monitor Finnish raptors and owls. Vår Fågelvärd. Suppl. 11: 187–190.

Saurola, P. 1987a. Bird ringing in Finland: status an guide-lines. Acta Reg. Soc. Sci. Litt. Gothoburgensis. Zoologica. 14: 189–201.

Saurola, P. 1987b. Mate and nest-site fidelity in Ural and Tawny Owls. In: Nero, R.W.; Clark, R.J.; Knapton, R.J.; Hamre, R.H., eds. Biology and conservation in northern forest owls: symposium proceedings; 1987 February 3-7; Winnipeg, MB. Gen. Tech. Rep. RM-142. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 81–86.

Saurola, P. 1989. Ural Owl. In: Newton, I., ed. Lifetime reproduction in birds. London, Great Britain: Academic Press: 327–345.

Saurola, P. 1992. Population studies of the Ural Owl *Strix uralensis* in Finland. In: Galbraith, C.A.; Taylor, I.; Percival, S., eds. The ecology and conservation of European owls. UK Nature Conserv. 5. Peterborough, Great Britain: Joint Nature Conservation Committee: 28–31.

Saurola, P., ed. 1995. Owls of Finland (in Finnish with short English summary). Kirjayhtymä Oy. Helsinki. Finland. 271 p.

Sulkava, S.; Huhtala, K. 1997. The Great Gray Owl (*Strix nebulosa*) in the changing forest environment of northern Europe. Journal of Raptor Research. 31: 151-159.

Abundance and Population Characteristics of Northern Spotted Owls (*Strix occidentalis caurina*) in Olympic National Park, Washington

D. Erran Seaman[1]

Abstract.—We monitored the threatened Northern Spotted Owl (*Strix occidentalis caurina*) in Olympic National Park from 1992 through 1996. We used a stratified random sampling scheme to survey 35 plots totalling 236 km^2, approximately 10 percent of the forested area of the park. We used mark-resight statistics to correct density estimates for owl pairs that were not detected on surveys. The east side of the park supported higher densities (0.15 pairs km^{-2}) than the west side (0.08 pairs km^{-2}) or the high elevation habitat (0 pairs km^{-2}). Park densities were twice as high as densities reported for surrounding harvested landscapes (USDA National Forest lands). Densities were significantly higher in the park interior than near the edge. The estimated park population is 230 pairs (± 71, 90 percent CI). We monitored reproductive success at approximately 60 territories annually. Fecundity fluctuated greatly; 3 years had high reproductive success and 2 years had no observed reproduction. Most monitored sites produced no fledglings in 2 to 5 years of monitoring. Fecundity in the national park was equal to or greater than fecundity reported for the surrounding national forest lands in all years. Analysis of owl pellets showed similar diets to those determined by other studies, flying squirrels (*Glaucomys sabrinus*) being the dominant prey item.

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Population Dynamics of Lanyu Scops Owls (*Otus elegans botelensis*)

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Abstract.—Monthly visits to Lanyu Island have been made to study Lanyu Scops Owls *(Otus elegans botelensis)* since 1986. This population has been surveyed by regular census and playback counts, by color banding, by monitoring the survival, reproduction and movements of individual owls, and by mapping and documenting the change in nest trees.

Annual playback counts of Lanyu Scops Owl from 1990 suggest that the population has been stable. The number of owls found each month fluctuated. The highest numbers of owls were seen at the beginning of the breeding season, while the lowest numbers were seen in September and October when owls were molting.

Some individuals lived 10 years after they were banded as adults. Given that most individuals do not enter the breeding population until 2 years of age, these individuals have very likely lived at least 12 years. Based on 12 years of data, on average only 37.5 percent of the fledglings survived to 1 year of age. After 1 year of age, survival rate varied between 78 percent and 95 percent.

The Lanyu Scops Owl starts breeding at 2 years of age. The number of owls remaining in the breeding population decreased with age, but their nesting success rates increased with age. Thus, for each age group, although the number of breeding owls decreased with age, most of the survivors could breed successfully (producing at least one young) at an older age. For owls that survived at least 5 years after banding, the number of fledglings each adult produced decreased with age. For the first 2 years, they fledged an average of 1.5 to 2 young. By the 4th to 6th year, this decreased to 1.1 and 1.2 young, respectively. After 8 years, success rate was reduced to zero.

Breeding success was limited by the availability of good nest cavities, and the success rate of owls using different cavities varied greatly. Nest cavities were natural tree cavities produced by rotting. The usability of these natural cavities change with age. Very few trees were used more than 4 years.

Dispersal is carried out primarily by juvenile females which moved significantly farther from their nest sites than males. Adults also moved between suitable breeding habitats, but the frequency and distances moved were not different between the sexes.

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Owls as Biomonitors of Environmental Contamination

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Abstract.—Much like the caged canary used by miners, a plethora of wildlife species have been promoted as biomonitors of environmental contamination. These species provide an "early warning system" for toxic contaminants in the environment. Species promoted as useful biomonitors share many common life history characters, such as wide distribution, territorial, non-migratory behavior, high trophic status, and high reproductive rates. Raptor species generally possess these characteristics. The Bald Eagle (*Haliaeetus leucocephalus*) and Osprey (*Pandion haliaetus*) have been widely used as biomonitors of aquatic contamination. However, few higher order consumers have been studied in detail or proposed for use in terrestrial systems. Exposure and effects of environmental contaminants on owls has been largely understudied. The studies done to date on owls and environmental contaminants have been conducted on both captive and wild owls, and have focused on a few selected species. Most of the captive studies have been conducted using Eastern Screech-owl (*Otus asio*) and Barn Owl (*Tyto alba*) colonies at the USFWS Patuxent Wildlife Research Center, Laurel, MD. The relatively few studies conducted on wild owls have included many different species, but have concentrated on the Great Horned Owl (*Bubo virginianus*), Barn Owl, and Eastern Screech-owl, and have focused heavily on analyzing contaminant levels (residue analyses) and post-mortem examination for cause of death of individual owls found dead. As higher order consumers, owls are susceptible to secondary poisoning and can bioconcentrate many different environmental contaminants through their prey. Owls have proven to be sensitive to a wide variety of toxic compounds, including pesticides, PCB's, metals, and fluoride, and are highly susceptible to secondary poisoning from consuming pesticide-poisoned prey. Endpoints examined include reproductive effects, eggshell thickness, residue analyses, cholinesterase inhibition, and induction of liver detoxifying enzymes. Much more work remains to be done using owls as biomonitors of environmental contamination, particularly with captive populations, salvaged individuals, raptor rehabilitation center birds, and with wild populations in areas around hazardous waste sites, smelters, landfills, agricultural croplands, and other major sources of environmental contamination.

In the field of wildlife toxicology, a plethora of wildlife species have been promoted as biomonitors, bioindicators, or sentinels, of environmental contamination (National Research Council 1991, Sheffield and Kendall, in press). Much like the caged canary used by miners, wildlife species today are being increasingly utilized as biomonitors of environmental health and overall quality. These species may provide an "early warning system" for toxic contaminants in the environment. Among the most attractive species for this purpose are the top predators. These species are positioned at the top of food chains and are in a position to be negatively impacted by secondary poisoning and bioaccumulation of contaminants in the environment. Within the birds of prey, species such as the Bald Eagle (*Haliaeetus leucocephalus*) and Osprey (*Pandion haliaetus*) have been closely studied, particularly with regard to their reproductive failure and subsequent population declines due to eggshell thinning. However, these species generally feed in aquatic environments. It is generally considered that birds are the most sensitive taxa to contaminants in terrestrial environments (Grue *et al.* 1983, Hoffman 1995). Few birds of prey have been studied in detail or proposed as a sentinel species for use in terrestrial systems. One notable exception to this is the Peregrine Falcon (*Falco peregrinus*), which has been studied extensively due to its dramatic populations declines and endangered status following reproductive failure from exposure to DDT and other organochlorine (OC) insecticides. However, peregrine populations have greatly increased in North America following the ban on DDT and other OCs, and the focus on Peregrine Falcons and contaminants has diminished to a large extent. Currently, owl species, as higher order consumers that take a wide variety of prey species, potentially are of great value as wildlife biomonitor species in terrestrial systems. Yet, owls have been relatively neglected in terms of wildlife toxicology studies (Blus 1996, Wiemeyer 1991). The studies done to date on owls and environmental contaminants have been conducted on both captive and wild owls, and have focused on a few selected species. Most of the captive studies have been conducted using Eastern Screech-owl (*Otus asio*) and Barn Owl (*Tyto alba*) colonies at the USFWS Patuxent Wildlife Research Center, Laurel, MD. The relatively few studies conducted on wild owls have included many different species, but have concentrated on the Great Horned Owl (*Bubo virginianus*), Barn Owl, and Eastern Screech-owl, and have focused heavily on analyzing contaminant levels (residue analyses) and post-mortem examination for cause of death of individual owls found dead. Secondary poisoning of owls that consumed prey tainted with anti-cholinesterase (anti-ChE) insecticides, anti-coagulant rodenticides, or other environmental contaminants is considered a significant route of exposure and can contribute significantly to owl mortality as well as to impaired reproduction and other sublethal effects (Grue *et al.* 1983, Blus 1996).

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The rationale for using owls as biomonitors of environmental contamination is that they possess many of the life history characteristics that are desirable of a good biomonitor species. These life history characteristics include: (1) high trophic level status (secondary consumer), (2) wide distribution, (3) territorial, generally non-migratory behavior, (4) high reproductive rates, (5) relatively easy to capture, handle, enumerate, (6) their biology is relatively well known, and (7) they are sensitive to a wide variety of environmental contaminants.

The objectives of this paper are to review and synthesize studies dealing with exposure and effects of environmental contaminants on owls worldwide, the use of owls as biomonitor (sentinel) species in wildlife toxicology studies, the possible role of environmental contaminants in the decline of owls, and to suggest future directions for research in these areas.

CATEGORIZATION OF STUDIES

This paper is divided into two categories, captive studies and field studies. These two categories are then further divided into more specific types of studies, including residue analysis studies, mortality (secondary poisoning), and effects.

Captive Studies

A vast majority of the captive studies on owls have been completed at the U.S. Fish and Wildlife Service's Patuxent Wildlife Research Center in Laurel, Maryland. Here, studies have been conducted examining exposure and possible effects of environmental contaminants, including secondary poisoning, in owls for over two decades. These studies have focused primarily on two species of owls, the Eastern Screech-owl and the Barn Owl.

Studies on Secondary Poisoning in Captive Owls

Secondary poisoning studies have focused on examining anti-coagulant rodenticides and highly toxic anti-ChE pesticides that are illegally broadcast to control predators (table 1). Generally, it has been found that owls are highly susceptible to secondary poisoning by anti-ChE insecticides and anti-coagulant rodenticides through the consumption of contaminated prey items. Effects found in these studies include both lethal and sublethal effects. Lethal effects were seen in owls exposed to organophosphate (OP) insecticides

Table 1.—*Studies examining secondary poisoning in captive owls.*

Species[1]	**Compound**	**Major findings**	**Author(s)**
TYAL	famphur	found signif. secondary poisoning, signif. plasma and brain ChE inhibition	Hill and Mendenhall (1980)
TYAL, BUVI, AEAC	six rodenticides	demonstrated potential secondary hazards of 4 of 6 rodenticides, sublethal effects seen (regurgitated blood, internal bleeding)	Mendenhall and Pank (1980)
STAL	warfarin	sublethal effects seen (dec. levels of plasma prothrombin), concludes that lethal effects would be unlikely	Townsend *et al.* (1981)
NYSC	Pb	mortality seen following feeding on prey containing lead shot	MacDonald *et al.* (1983)
TYAL	flocoumafen	20% (1 of 5) dosed birds died in 6 days	Newton *et al.* (1994)
TYAL	brodifacoum, flocoumafen	4 of 6 dosed owls died in 1 day trial with brodifacoum, 1 of 5 died in 6 day trial with flocoumafen	Wyllie (1995)
OTAS	carbofuran, fenthion	mortality, signif. depression in brain ChE activity	Vyas *et al.* (unpubl. data, pers. comm.)

[1] See Appendix 1.

(Hill and Mendenhall 1980, N. Vyas pers. comm.), rodenticides (Mendenhall and Pank 1980, Newton *et al.* 1994, Wyllie 1995), and lead shot (MacDonald *et al.* 1983). Sublethal effects seen included regurgitated blood and internal bleeding (Mendenhall and Pank 1980) and decreased levels of plasma prothrombin (Townsend *et al.* 1981) from anti-coagulant rodenticides, and plasma and brain ChE inhibition (Hill and Mendenhall 1980, N. Vyas pers. comm.) for anti-ChE insecticides.

Studies on Effects in Captive Owls

Captive studies on possible effects of environmental contaminants have focused on the OC insecticides (e.g., endrin, kelthane, DDE), PCBs, and fluoride; however, OP (EPN, fenthion, monocrotophos) and carbamate (carbofuran) insecticides, cyanide, lead, and selenium have also been studied (table 2). Dietary exposure to relatively low levels of the OC insecticides DDE and kelthane have been shown to cause severe reproductive effects such as eggshell thinning, egg breakage, embryonic mortality, and reduced reproductive productivity (McLane and Hall 1972, Mendenhall *et al.* 1983). Dietary exposure to low levels of the OC insecticide endrin was not found to result in eggshell thinning, but was found to cause a significant decrease in hatching success (Fleming *et al.* 1982). Although low dietary levels of a PCB congener were found to result in no apparent reproductive effects (McLane and Hughes 1980), an interperitoneal (i.p.) exposure to a PCB congener resulted in induction of the mixed-function oxidases (MFOs) system (cytochrome P450) as well as liver hemorrhages and hepatomegaly (Rinsky and Perry 1981). Dietary fluoride was found to result in elevated fluoride concentrations in bone and eggshells, significantly decreased hatching success and an overall impairment of reproduction, morphological (shorter tibiotarsus and radius-ulna lengths) and biochemical (plasma phosphorus levels) abnormalities, and significantly decreased egg and hatchling weights (Hoffman *et al.* 1985, Pattee *et al.* 1988). Cyanide was found to be acutely lethal to owls at extremely low doses, and elevated levels of cyanide in blood allowed for easier detection of cyanide poisoning than other tissues (Wiemeyer *et al.* 1986). Selenium at levels known to occur in small mammals at Kesterson NWR in California was found to cause morphological abnormalities (decreased femur lengths), biochemical changes in the liver (activation of the glutathione system,

Table 2.—*Studies examining effects of environmental contaminants on captive owls.*

Species[1]	Compound	Major findings	Author(s)
OTAS	DDE	signif. eggshell thinning (13%) from diet of 10 ppm dry wt.	McLane and Hall (1972)
BUBU, 26 other indiv. (species not given)	dieldrin	28 owls died mysteriously; dieldrin-treated lumber used for shavings in cages of rodents fed to owls linked to at least 20 of the deaths	Jones *et al.* (1978)
OTAS	PCBs	Aroclor 1,248 fed (3 mg/kg) to owls - no effects on eggshell thickness, no. of eggs laid, young hatched or fledged	McLane and Hughes (1980)
TYAL	PCBs	injection of 30 mg/kg Aroclor 1254 resulted in induction of MFO system (cytochrome P450), liver hemorrhages and hepatomegaly seen	Rinsky and Perry (1981)
OTAS	endrin	owls fed 0.75 ppm endrin produced 43% fewer fledged owlets than controls; hatching success appeared to be main repro. variable affected; no eggshell thinning seen	Fleming *et al.* (1982)
TYAL	DDE, dieldrin	owls fed diet containing 3.0 ppm DDE, 0.5 ppm dieldrin, or both; DDE caused signif. eggshell thinning, egg breakage, embryonic mortality, reduced repro. productivity; dieldrin caused slight (but signif. eggshell thinning, no signif. reduction in breeding success	Mendenhall *et al.* (1983)
OTAS	fluoride	owls fed diet containing 0, 40, or 200 ppm fluoride; at 40 ppm, signif. smaller egg volume, shorter tibiotarsus length and higher plasma P seen, at 200 ppm, signif. lower egg wts., lengths, shorter tibiotarsus and radius-ulna lengths seen, day 1 hatchling weight about 10% less than controls; overall signif. repro. impairment seen	Hoffman *et al.* (1985)
OTAS	sodium cyanide	owls given 6, 12, 24, or 48 mg/kg sodium cyanide in gelatin capsule placed in proventriculus; LD50 8.6 mg/kg, elevated blood cyanide levels found, blood superior to liver as tissue of choice for detecting cyanide exposure	Wiemeyer *et al.* (1986)
OTAS	fluoride	owls fed 0, 40, or 200 mg/kg; hatching success neg. impacted at 200 mg/kg, eggshell thickness not affected, fluoride concs. elevated in bone and eggshells, large variations among indivs.	Pattee *et al.* (1988)
OTAS	kelthane	owls fed diet containing 10 ppm kelthane (with or without DDT-related contams.); eggshell wt. and thickness index signif. lower for both dosed groups, eggshell thickness signif. lower for kelthane w/o DDT impurities than for controls, signif. dec. in % of eggs hatching for owl pairs w/no nesting experience	Wiemeyer *et al.* (1989)
OTAS	EPN, fenthion, carbofuran, monocrotophos	acute toxicity high (LD50's 1.5-3.9 mg/kg) for all compounds, brain ChE activity depressed >65% for all compounds in owls that died within 24 hrs.	Wiemeyer and Sparling (1991)
OTAS	selenium	owls fed diets containing 0. 4.4, or 13.2 ppm (wet wt.) Se; at 4.4 ppm, no malformed nestlings, but femur lengths of young signif. dec., liver biochem. (glutathione/lipid peroxidation) neg. affected in 5 day old nestlings; at 13.2 ppm, adult mass and repro. success dec. signif.	Wiemeyer and Hoffman (1996)

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[1] See Appendix 1.

increased liver peroxidation), and a significant decrease in adult mass and reproductive success (Wiemeyer and Hoffman 1996).

Field Studies

Residue Analyses in Wild Owl Tissues

Residue analysis studies have been relatively numerous and wide-ranging in owls (table 3). A vast majority of these studies have been conducted in North America (US, Canada), but studies in Europe (The Netherlands, Norway, Spain, UK) and Africa (South Africa) have also been done. Many different owl species have been used in these studies—everything from small owls (*Otus asio*) to large owls (*Bubo bubo*). The largest data bases found for contaminant residues in owls are for *Bubo virginianus* (11 studies), *Tyto alba* (10 studies), *Asio otus* (six

Table 3.—*Studies examining contaminant residues in wild owls.*

Species[1]	**Contaminants**	**Location**	**Author(s)**
ASOT, TYAL	OCs/PCBs	The Netherlands	Koeman and van Genderen (1966)
ASFL, BUVI, SPCU	Hg	Canada (Alb., Sask.)	Fimreite *et al.* (1970)
BUVI	OCs/PCBs	Canada (Ontario)	Postupalsky (1970)
STAL	OCs/PCBs	Denmark	Karlog *et al.* (1971)
BUVI (eggs, juv., adults)	OCs/PCBs	US (Montana)	Seidensticker and Reynolds (1971)
ASOT, TYAL	OCs/PCBs	The Netherlands	Fuchs *et al.* (1972)
BUVI	OCs/PCBs	US (Texas)	Flickinger and King (1972)
OTAS (eggs)	OCs/PCBs	US (Ohio)	Klaas and Swineford (1976)
STAL, TYAL	Hg	United Kingdom	Stanley and Elliott (1976)
BUVI, OTAS (eggs)	OCs	US (New York)	Lincer and Clark (1978)
TYAL	OCs/PCBs	US (Maryland)	Klaas *et al.* (1978)
ASCA, ASFL, BUAF, BUVI, TYAL, TYCA	OCs/PCBs	Canada, South Africa	Peakall and Kemp (1980)
BUVI	OCs/PCBs	US (Ohio)	Springer (1980)
BUVI	OCs	US (New York)	Stone and Okoniewski (1983)
OTKE	heptachlor	US (Oregon)	Henny *et al.* (1984)
AEAC, ASFL, ASOT, BUVI, OTAS, STVA	OCs/PCBs	US (Illinois)	Havera and Duzan (1986)
OTAS, BUVI, STVA, TYAL	OCs/PCBs	US (Florida)	Sundlof *et al.* (1986)
AEFU, ASFL, ASOT BUBU, GLPA, STAL, SUUL	Hg, OCs/PCBs	Norway	Froslie *et al.* (1986)

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Species[1]	Contaminants	Location	Author(s)
TYAL	OCs	Spain	Sierra and Santiago (1987)
ASFL, ASOT, BUVI, NYSC, SPCU, STNE	Hg, OCs/PCBs	Canada	Noble and Elliott (1990)
OTAS	OCs/PCBs	Canada (Ontario)	Frank and Braun (1990)
TYAL	Cd, Cu, Pb, Zn	The Netherlands	Denneman and Douben (1993)
ASOT, BUBU, OTSC STAL, TYAL	Pb	France	Pain and Amiard-Triquet (1993)
BUVI, OTKE	Pb, Cd	US (Idaho)	Henny *et al.* (1994)
TYAL	Cd, Cu, Pb, Mn, Fe	The Netherlands	Esselink *et al.* (1995)
TYAL	As	US (Texas)	Sheffield and McClure (in review)
BUVI	dieldrin	US (Colorado)	Hoff (pers. comm.)

[1] See Appendix 1.

studies), *Asio flammeus* (five studies), and *Otus asio* (five studies). Contaminants studied in owls include metals (mostly Hg, Pb, and Cd), metalloids (As, Se), OC insecticides, and PCBs. It is not possible to generalize the patterns of contaminants found in owls, but relatively high levels of contaminants have been found in owl eggs and tissues in many different contaminated areas. Recently, several studies have successfully used non-lethal methods to examine exposure to contaminants on owls, including residue analysis of primary feathers for assessing detectable metal burdens in owls from contaminated sites (Denneman and Douben 1993, Esselink *et al.* 1995, Sheffield and McClure, unpubl. data) and blood and fecal samples for analyzing OP insecticide exposure and plasma ChE activity (Buck *et al.* 1996).

Accounts of Mortality (Secondary Poisoning) in Wild Owls

There have been a number of accounts of mortality through secondary poisoning in wild owls (table 4). Post-mortem examinations of individual owls have found that insecticides and rodenticides have been responsible for many deaths, and it should be kept in mind that there may be a multitude of undetected owl mortality incidents for every one observed. The rodenticide thallium sulfate was found to cause secondary poisoning in owls in Germany (Steininger 1952) and Denmark (Clausen and Karlog 1977). Several anti-ChE insecticides (OPs and carbamates) have been implicated in mortalities of wild owl species. In Israel, a mass mortality of raptors, including *Tyto alba*, *Asio otus*, and *Asio flammeus*, occurred from feeding on contaminated prey following application of the OP insecticide monocrotophos (Mendelssohn and Paz 1977). The OP insecticide famphur, used on cattle, was found to cause tertiary mortality in a Great Horned Owl in Oregon (Henny *et al.* 1987). A number of Great Horned Owls throughout the U.S. were found to have been poisoned by anti-ChE insecticides, including phorate, fenthion, and carbofuran (Franson and Little 1996). The major component of the avicide Rid-a-Bird, the OP insecticide fenthion, has been found to cause mortality in many species of owls in North America, including Snowy Owls (*Nyctea scandiaca*), Short-eared Owls (*Asio flammeus*), and Great Horned Owls (*Bubo virginianus*). In Kenya, Africa, Keith and Bruggers (in press) report on raptor mortalities from fenthion poisoning used to control Quelea (*Quelea quelea*) colonies. Owls found to have died from fenthion poisoning include Cape Eagle Owls

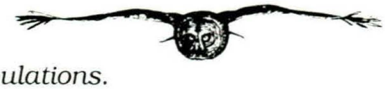

Table 4.—*Accounts of mortalities (secondary poisoning) in wild owl populations.*

Species[1]	Compound	Major findings	Location	Author(s)
ATNO, TYAL	thallium sulfate	dead ATNO and TYAL found following thallium use to control rodents	Germany	Steininger (1952)
STVA	heptachlor	one indiv. found dead in pasture sprayed with heptachlor	US (Mississippi)	Ferguson (1964)
ASOT, TYAL	Hg, dieldrin, aldrin, heptachlor	several dead indivs. found	The Netherlands	Koeman *et al.* (1969)
BUVI	aldrin	one indiv. found dead in aldrin-treated rice field	US (Texas)	Flickinger and King (1972)
ASFL, ASOT, TYAL	monocrotophos	dead or dying (ASFL 5, ASOT 2, TYAL 22), and paralyzed but recovered (ASFL 4, ASOT 2, TYAL 10) owls found	Israel	Mendelssohn and Paz (1977)
STAL	thallium sulfate	dead STAL found following thallium use to control rodents	Denmark	Clausen and Karlog (1977)
NYSC, BUVI	strychnine	dead NYSC(3) and BUVI(1) found having fed on pigeons that fed on strychnine-laced corn	US (Minnesota)	Redig *et al.* (1982)
BUVI	chlordane	BUVI(1) found dead	US (Oregon)	Blus *et al.* (1983)
TYAL	brodifacoum	no mortality found, only one TYAL with residues after use of brodifacoum on farms to control rats and mice; little exposure due to TYAL prey choice (meadow voles)	US (New Jersey)	Hedgal and Blaskiewicz (1984)
OTAS, TYAL	brodifacoum	dead OTAS (1) found, owls and voles contained signif. brodifacoum residues, OTAS (1) found with sublethal clotting	US (Virginia)	Merson *et al.* (1984)
TYAL	brodifacoum	mass mortalities in palm-oil plantations after TYAL fed on rodents	Malaysia	Duckett (1984)
BUVI	dieldrin	BUVI(1) found to have lethal levels (1974-81)	US (Illinois)	Havera and Duzan (1986)
BUVI	famphur	one indiv. found dead near cattle feedlot, brain ChE activity depressed 85%, suspected tertiary poisoning - owl ate Red-tailed Hawk that ate magpie	US (Oregon)	Henny *et al.* (1987)
ASOT, BUVI, OTAS, STVA	brodifacoum	owl species living in vicinity of apple orchard impacted by brodifacoum; 32 of 38 OTAS exposed, 6 OTAS mortalities, one ASOT mortality	US (Virginia)	Hedgal and Colvin (1988)
BUVI, OTAS, TYAL	OC insecticides	BUVI found to have died from exposure to chlordane (4), dieldrin (1), dieldrin and chlordane (2), and mixture of OCs (6); TYAL(1) and OTAS(1) died from dieldrin exposure (1982-1986)	US (New York)	Stone and Okoniewski (1988)

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Species[1]	Compound	Major findings	Location	Author(s)
BUVI, TYAL	endrin	BUVI(1) and TYAL(4) found dead	US (Washington)	Blus *et al.* (1989)
SPCU	carbofuran	carbofuran sprayed to control grasshoppers had signif. impact on Burrowing Owl survival and repro. success; 27% dec. in repro. success in nests sprayed within 50 m	Canada	Fox *et al.* (1989)
OTAS	OC insecticides	OTAS(1) found with lethal levels of a mixture of OC insecticides	Canada (Ontario)	Frank and Braun (1990)
TYAL	brodifacoum, difenacoum	145 owl carcasses examined (1983-1989); 10% found with rodenticide residues (one or the other or both)	UK	Newton *et al.* (1990)
TYAL	aldrin/dieldrin	627 owls autopsied, poisoning found in 8.8% of owls (up to 40% of all mortalities in some agricultural areas from 1963-1977)	UK	Newton *et al.* (1991)
BUVI, OTAS, STVA	OP, carbamate insecticides	105 owl carcass examined for cause of death and brain ChE activity; 5.7% found to have died from anti-ChE insecticides	US (Illinois)	Gremillion-Smith and Woolf (1993)
BUVI, OTAS, TYAL	chlordane, dieldrin	BUVI(9), TYAL(1), and OTAS(3) found to have died from exposure to chlordane, BUVI(2) died from dieldrin (1986-1990)	US (New York, Maryland)	Okoniewski and Novesky (1993)
TYAL	rodenticides (4)	353 owl carcasses examined (1990-1994); only 1.4% died from rodenticide poisoning, but 32% of carcasses contained residues	UK	Wyllie (1995)
BUVI	OC, OP insecticides, H_2S	132 owl carcasses examined for cause of death; 8% found to have died from exposure to toxic chemicals	US (24 states)	Franson and Little (1996)
BUVI	dieldrin	subacute exposure to dieldrin found to kill a large but unknown no. of juv. and adult owls from 1994-1996 (residues found in blood, brain, liver)	US (Colorado)	D. Hoff (pers. comm.)
ASFL	carbofuran	ASFL(1) found dead	US (Utah)	L. Lyon (unpubl. data)
BUVI	carbofuran	BUVI(1 each) found dead in VA(1987), DE (1989), IA (1990)	US (Virginia, Iowa, Delaware)	L. Lyon (unpubl. data)
ASFL	fenthion	ASFL(1) found dead	US (Washington)	M. Marsh (pers. comm.)
BUVI	fenthion	BUVI(1) found dead (1996)	US (Washington)	M. Marsh (pers. comm.)
NYSC	fenthion	NYSC(1) found dead	US (Illinois)	M. Marsh (pers. comm.)
TYAL	phorate	TYAL(1) found dead (1989)	US (Wisconsin)	J. Spinks (unpubl. data)
ASOT, BUVI OTAS, TYAL	OC insecticides, PCBs	lethal levels found in numerous BUVI, ASOT, OTAS, and TYAL (OC mixtures and PCBs) in late 1980s	US (New York)	W. Stone (pers. comm.)
NYSC	fenthion	NYSC(at least 1) found dead at airport	US (Virginia)	N. Vyas (pers. comm.)

[1] See Appendix 1.

(*Bubo capensis*), Giant Eagle Owls (*Bubo bubo*), and a Pearl-spotted Owlet (*Glaucidium perlatum*). In New York, many individual Great Horned Owls, Barn Owls, and Eastern Screech-owls have been found to have died from OC insecticide exposure, including DDE, dieldrin, chlordane, heptachlor, and PCBs, since the early 1980's (Stone and Okoniewski 1983, Okoniewski and Novesky 1993, W.B. Stone pers. comm.). At the Rocky Mountain Arsenal in Colorado, numerous juvenile and adult Great Horned Owls were found to have died from exposure to high levels of the OC insecticide dieldrin, a soil contaminant at the site.

Several studies have examined cause of death in owls through post-mortem necropsy of owl carcasses accumulated over a number of years. In the U.S., an examination of 132 Great Horned Owl carcasses revealed that about 8 percent of them were killed by toxic chemical poisoning, mainly insecticides (Franson and Little 1996). Also in the U.S., 105 owl carcasses (Great Horned Owl, screech owl, Barred Owl (*Strix varia*)) from central and southern Illinois were examined for cause of death and brain ChE activity (Gremillion-Smith and Woolf 1993). They determined that at least six (5.7 percent) of the owls may have died from anti-ChE insecticide poisoning, including two adult Great Horned Owls whose brain ChE activities were depressed 53 percent and 69 percent of normal activities and one subadult screech owl whose brain activity was depressed 60 percent of normal activity.

In the UK, secondary poisoning of Barn Owls by anti-coagulant rodenticides has been closely examined. Newton *et al.* (1990) examined brodifacoum and difenacoum exposure in Barn Owls from the UK, and of the 145 owls tested from 1983-1989, 10 percent were found to have rodenticide residues (one or the other or both). A study of 627 Barn Owl carcasses from the UK revealed that about 9 percent of these owls were poisoned by the OC insecticide aldrin/dieldrin, although up to 40 percent of all mortalities in some agricultural areas resulted from aldrin/dieldrin poisoning (Newton *et al.* 1991). Wyllie (1995) analyzed 353 carcasses of Barn Owls from 1990-1994, and found that, although only 1.4 percent of owls died from poisoning, 32 percent of the owls contained rodenticide residues.

Studies of Secondary Poisoning in Wild Owls

Several studies have been carried out specifically to test the secondary poisoning hazards of trial rodenticides on non-target species. The anti-coagulant rodenticide brodifacoum has been the focus of several studies in wild owls. Hedgal and Blaskiewicz (1984) found that Talon (50 ppm brodifacoum), used to control house mice and rats, did not cause mortality in Barn Owls from New Jersey. Residues were found in only one Barn Owl. However, as these Barn Owls fed mostly on meadow voles (*Microtus pennsylvanicus*) and did not spend much time hunting in and around farms, it is not surprising that no mortality was seen. Merson *et al.* (1984) examined brodifacoum exposure to owls from its use in controlling voles in a Virginia apple orchard. Three screech owls and one Barn Owl inhabiting the orchard area were fit with radio-transmitters. One screech owl died, one screech owl had large subcutaneous blood clot on left side of breast, voles contained significant brodifacoum residues, and two screech owls contained brodifacoum residues, indicating that secondary poisoning of the screech owl population in vicinity of orchard occurred. In a similar but more extensive study, Hedgal and Colvin (1988) used radiotelemetry to examine brodifacoum (10 ppm) exposure in Eastern Screech-owls (38), Barred Owls (five), Great Horned Owls (two), and Long-eared Owls (two) living in the vicinity of an apple orchard. They found that 32 screech owls were exposed to brodifacoum, six died from the exposure, four of the six live screech owls contained brodifacoum residues, and one Long-eared Owl died from brodifacoum poisoning.

Studies on Sublethal Effects in Wild Owls

Few studies have examined exposure and possible sublethal effects of environmental contaminants in wild owl populations (table 5). Eggshell thinning due to exposure to OC insecticides has been examined in owls in the U.S. (Hickey and Anderson 1968, Klaas and Swineford 1976, Springer 1980) and Australia (Olsen *et al.* 1993). In California, Hickey and Anderson (1968) found no significant changes in eggshell weights in Great Horned Owl eggs collected from 1886-1936 and 1948-1950. Springer (1980) compared addled and viable Great Horned Owl eggs from Ohio for pesticide

Table 5.—*Studies of sublethal effects of contaminants in wild owl populations.*

Species[1]	Compounds	Major findings	Author(s)
BUVI	OCs	no signif. eggshell thinning (small "n")	Hickey and Anderson (1968)
BUVI	OCs	eggshells showed slight inc. in thickness and weight (n=3)	Seidensticker and Reynolds (1971)
TYAL	OCs	reproductive success	Klaas *et al.* (1978)
SPCU	carbofuran, carbaryl	reproductive success	James and Fox (1987), Fox *et al.* (1989)
TYAL, TYLO TYNO, TYTE, NIRU, NIST, NICO	OCs	signif. eggshell thinning found in TYNO and NIST	Olsen *et al.* (1993)
BUVI	OP insecticides	plasma ChE activity and fecal urates measured, no signif. exposure in corn crops, non-treated habitat and wide diversity of prey limited exposure	Buck *et al.* (1996)
TYAL	arsenic	altered feeding habits (insects preferred); dec. repro. success (#eggs hatched/nest, # young fledged/nest)	Sheffield and McClure (unpubl. data)

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[1] See Appendix 1.

levels and eggshell parameters, and found that addled eggs contained consistently higher pesticide levels and were an average of 5 percent thinner. No differences in eggshell thickness was found in screech owl eggs from pre-1947 and from 1973 (Klaas and Swineford 1976). In Montana, Great Horned Owl eggs were found to have relatively low levels of OC insecticide residues and no significant changes in eggshell weight and thickness were found between pre-1946 and 1967 samples (Seidensticker and Reynolds 1971). In New York, relatively high DDE residues were found in screech owl and Great Horned Owl eggs, and eggshell thickness of Great Horned Owl eggs was found to be significantly less than that of pre-DDT era eggshells (Lincer and Clark 1978). In Australia, Olsen *et al.* (1993) found that average eggshell thickness significantly decreased (by 6.3 percent) in the Southern Boobook Owl (*Ninox novaeseelandiae*), and strongly decreased in the Powerful Owl (*Ninox strenua*), after the introduction of DDT to Australia. Eggshell thickness for six other owl species was not found to differ significantly, but sample sizes for most species were small.

Beyond eggshell thinning, few studies have attempted to assess exposure and potential effects of environmental contaminants on wild owl populations. Klaas *et al.* (1978) examined OC insecticide residues and reproductive success in Barn Owls from Chesapeake Bay, Maryland. In 18 nests, they found relatively high levels of DDE, PCBs and dieldrin in eggs and found significant eggshell thinning (5.5 percent) when compared to eggshells from pre-DDT times. Eggshell thickness was found to be inversely correlated with concentrations of DDE, DDD, and dieldrin residues. Reproductive productivity of these Barn Owls was found to be lower than that needed to maintain a stable population, and it was calculated that at least 15 percent of the Barn Owl population had contaminant residue burdens high enough to be detrimental to their reproduction. Following the finding of OP insecticide residues in *Peromyscus* spp. in Iowa cornfields, Buck *et al.* (1995) examined potential exposure of Great Horned Owls to OP insecticides. They used radio-telemetry and non-lethal sampling techniques, analyzing blood plasma for ChE activity and fecal samples for fecal urates (OP metabolites). Of the 27 individual owls followed, three had plasma ChE activities that were significantly less than those of controls. However, they concluded that the large proportion of non-treated habitat within owl home ranges and the diversity of prey consumed limited OP insecticide exposure in the Great Horned Owls monitored. James and Fox (1987) and Fox *et al.* (1989) found that the anti-ChE insecticide carbofuran, applied to control grasshoppers, significantly impacted Burrowing Owl (*Speotyto cunicularia*) survival and reproductive success when sprayed over nest burrows. In addition, they found a 27 percent decrease in reproductive success in nests where carbofuran was sprayed within 50 m of the nest. The results suggested that the negative impacts were a result of toxicity rather than food removal. Sheffield and McClure (unpubl. data) found that Barn Owls living on an arsenic-contaminated hazardous waste site in Texas showed altered prey selection (preferring katydids over mammals) and decreased reproductive success when compared to clean sites in Texas. Although the number of eggs/clutch was not significantly different, the number of eggs hatched and the number of young fledged per nest were significantly lower than Barn Owls from clean sites and were closer to the averages found in Barn Owls at a DDE-contaminated site (Klaas *et al.* 1978).

DISCUSSION

Many different types of contaminants have been studied in owls, including OC insecticides (DDT and its metabolites, dieldrin, endrin, kelthane, etc.), OP insecticides (chlorpyrifos, terbufos), PCB's, heavy metals (Hg, Pb) metalloids (As, Se), fluoride, and a number of rodenticides (warfarin, brodifacoum, etc.). In the studies outlined above, many different endpoints of contamination have been studied in owls, including bioaccumulation (residue analysis), secondary poisoning, biochemical (ChE inhibition, MFO induction), reproductive (eggshell thinning, productivity), and ecological (dietary changes, etc.). Owls have proven to be among the most sensitive avian species to a number of different environmental contaminants, but have been underused as sentinel species to this point. Owl species should serve as key sentinel species in any evaluation of exposure and possible effects of environmental contamination.

Declines of Owls and Possible Role of Contaminants

It is possible that owl population declines over the last several decades are linked directly to the increased rate of pesticide use over that time, but few studies have examined this issue. Therefore, this is an area that needs further study currently. Several species of owls around the world have been in slow or rapid decline since the mid-1900's when pesticide use dramatically increased. Among these are the Barn Owl in the United States, whose populations have drastically decreased in the agroecosystems of the Great Lakes and midwestern states (Colvin 1985, Marti 1992). Populations of the Burrowing Owl currently are facing problems in North America due mainly to habitat destruction and alteration, although no studies have been conducted to examine a possible role of pesticides in the declines. From the study by Fox *et al.* (1989) in the Prairie Provinces of Canada, it is likely that pesticides are at least partly responsible for the decline. High levels of OC insecticides, PCBs and Hg have been found in eggs and tissues of arctic owls (e.g., Snowy Owl, Great Gray Owl (*Strix nebulosa*), northern populations of Great Horned Owl), who tend to move great distances between seasons and whose populations fluctuate greatly (Noble and Elliott 1990). However, recent residue data for arctic owls is not available and a possible connection between contaminants and population health, fluctuations, and declines in these owls has not been studied. In addition to this, several other North American owls are declining including the Elf Owl, Ferruginous Pygmy-owl, Spotted Owl, and Short-eared Owl (White 1994). While habitat destruction and alteration may serve as the major factor in these declines, the role of widespread pesticide use must not be discounted and should be investigated.

Future Research Directions and Conclusions

There are several different directions for future research on owls and environmental contaminants to follow. Among these are:

1. Continued captive studies are required. Captive studies are relatively expensive, and few facilities are equipped to conduct studies such as this. It is important to attempt to determine the extent of exposure and possible hazard of rodenticides and insecticides in wild owls using captive animals.

2. It is important to systematically monitor for dead owls and to salvage dead owls for examination. This is a common practice in parts of Europe (e.g., The Netherlands, UK), but a greater effort needs to be put forth in other parts of world.

3. There is a need for greater use of radiotelemetry in following the fate of wild owls and their exposure and effects of contaminants.

4. The continued use and development of biomarkers of exposure in owls and their relation to impending biological effects is of great importance.

5. Greater use of non-lethal techniques, such as the use of feathers, eggshells, and blood and fecal samples, to monitor exposure to environmental contaminants should be considered important and will allow continued monitoring of the same live individuals over time while not impacting owl populations.

6. Raptor rehabilitation facilities hold a lot of promise for monitoring exposure and effects of contaminants in owls as well as other raptors. Injured and dead owls are brought to these facilities routinely, and monitoring exposure to contaminants will allow us some insight into potential environmental problems.

7. It is of importance to monitor wild populations of owls at such locations as hazardous waste sites, industrial areas, agricultural areas, landfills, mining areas, and other potentially contaminated sites. As relatively sensitive sentinel species, owls can provide an early warning to potential environmental health hazards.

8. We need to expand international efforts of monitoring contaminants in owls. As many hazardous pesticides and other chemicals are currently being used around the world, mass dieoffs of birds are still occurring in some locations (e.g., Dickcissels (*Spiza americana*) in Venezuela, Swainson's Hawks (*Buteo swainsoni*) in Argentina, Mississippi Kites (*Ictinia mississipiensis*) in Columbia). Continental monitoring, identifying areas of high probability of exposure, is important and should be implemented.

9. Ultimately, the question of whether or not owls (as sensitive, non-target, predatory species) are adequately protected by regulations on toxic chemicals in the environment needs to be answered.

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LITERATURE CITED

Blus, L.J. 1996. Effects of pesticides on owls in North America. Journal of Raptor Research. 30: 198-206.

Blus, L.J.; Henny, C.J.; Grove, R.A. 1989. Rise and fall of endrin usage in Washington state fruit orchards: effects on wildlife. Environment Pollution. 60: 331-349.

Blus, L.J.; Pattee, O.H.; Henny, C.J.; Prouty, R.M. 1983. First records of chlordane-related mortality in wild birds. Journal of Wildlife Management. 47: 196-198.

Buck, J.A.; Brewer, L.W.; Hooper, M.J.; Cobb, G.P.; Kendall, R.J. 1996. Monitoring Great Horned Owls for organophosphorus pesticide exposure in agricultural areas of south-central Iowa. Journal of Wildlife Management. 60: 321-331.

Clausen, B.; Karlog, O. 1977. Thallium loading in owls and other birds of prey in Denmark. Nord. Veterinaermed. 29: 227-231.

Colvin, B.A. 1985. Common Barn Owl population decline in Ohio and the relationship to agricultural trends. Journal of Field Ornithology. 56: 224-235.

Denneman, W.D.; Douben, P.E.T. 1993. Trace metals in primary feathers of the Barn Owl (*Tyto alba guttatus*) in the Netherlands. Environment Pollution. 82: 301-310.

Duckett, J.E. 1984. Barn Owls (*Tyto alba*) and the "second generation" rat-baits utilized in oil palm plantations in peninsular Malaysia. Planter (Kuala Lumpur). 60: 3-11.

Esselink, H.; van der Geld, F.M.; Jager, L.P.; Posthuma-Trumpie, G.A.; Zoun, P.E.F.; Baars, A.J. 1995. Biomonitoring heavy metals using the Barn Owl (*Tyto alba guttata*): sources of variation especially relating to body condition. Archives of Environmental Contamination and Toxicology. 28: 471-486.

Ferguson, D.E. 1964. Some ecological effects of heptachlor on birds. Journal of Wildlife Management. 28: 158-162.

Fimreite, N.; Fyfe, R.W.; Keith, J.A. 1970. Mercury contamination of Canadian prairie seed eaters and their avian predators. Canadian Field-Naturalist. 84: 269-274.

Fleming, W.J.; McLane, M.A.R.; Cromartie, E. 1982. Endrin decreases Screech Owl productivity. Journal of Wildlife Management. 46: 462-468.

Flickinger, E.L.; King, K.A. 1972. Some effects of aldrin-treated rice on Gulf Coast wildlife. Journal of Wildlife Management. 36: 706-727.

Fox, G.A.; Mineau, P.; Collins, B.; James, P.C. 1989. The impact of the insecticide carbofuran (Furadan 480F) on the Burrowing Owl in Canada. Tech. Rep. Ser. 72. Ottawa, Ontario, Canada: Canadian Wildlife Service.

Frank, R.; Braun, H.E. 1990. Organochlorine residues in bird species collected dead in Ontario 1972-1988. Bulletin of Environmental Contamination and Toxicology. 44: 932-939.

Franson, J.C.; Little, S.E. 1996. Diagnostic findings in 132 Great Horned Owls. Journal of Raptor Research. 30: 1-6.

Froslie, A.; Holt, G.; Norheim, G. 1986. Mercury and persistent chlorinated hydrocarbons in owls *Strigiformes* and birds of prey *Falconiformes* collected in Norway during the period 1965-1983. Environment Pollution. (Ser. B) 11: 91-108.

Fuchs, P.; Rooth, J.; DeVos, R.H. 1972. Residue levels of persistent chemicals in birds of prey and owls in the Netherlands in the period from 1965-1971. TNO-Nieuws. 10: 532-541.

Gremillion-Smith, C.; Woolf, A. 1993. Screening for anticholinesterase pesticide poisoning in Illinois raptors. Transactions of the Illinois Academy of Science. 86: 63-69.

Grue, C.E.; Fleming, W.J.; Busby, D.G.; Hill, E.F. 1983. Assessing hazards of oraganophosphate insecticides to wildlife. Transactions of the North American Wildlife Natural Resource Conference. 48: 200-220.

Havera, S.P.; Duzan, R.E. 1986. Organochlorine and PCB residues in tissues of raptors from Illinois, 1966-1981. Bulletin of Environmental Contamination and Toxicology. 36: 23-32.

Hedgal, P.L.; Blaskiewicz, R.W. 1984. Evaluation of the potential hazard to Barn Owls of talon (brodifacoum bait) used to control rats and house mice. Environmental Toxicology and Chemistry. 3: 167-179.

Hedgal, P.L.; Colvin, B.A. 1988. Potential hazard to Eastern Screech-owls and other raptors of brodifacoum bait used for vole control in orchards. Environmental Toxicology and Chemistry. 7: 245-260.

Henny, C.J.; Blus, L.J.; Hoffman, D.J.; Grove, R.A. 1994. Lead in hawks, falcons and owls downstream from a mining site on the Couer d'Alene River, Idaho. Environmental Monitoring Assessment. 29: 267-288.

Henny, C.J.; Blus, L.J.; Kaiser, T.E. 1984. Heptachlor seed treatment contaminates hawks, owls and eagles of Columbia Basin, Oregon. Journal of Raptor Research. 18: 41-48.

Henny, C.J.; Kolbe, E.J.; Hill, E.F.; Blus, L.J. 1987. Case histories of bald eagles and other raptors killed by organophosphorus insecticides topically applied to livestock. Journal of Wildlife Disease. 23: 292-295.

Hickey, J.J.; Anderson, D.W. 1968. Chlorinated hydrocarbons and eggshell changes in raptorial and fish-eating birds. Science. 162: 271-273.

Hill, E.F.; Mendenhall, V.M. 1980. Secondary poisoning of Barn Owls with famphur, an organophosphate insecticide. Journal of Wildlife Management. 44: 676-681.

Hoffman, D.J. 1995. Wildlife toxicity testing. In: Hoffman, D.J.; Rattner, B.A.; Burton, G.A., Jr.; Cairns, J. Jr., eds. Handbook of ecotoxicology. Boca Raton, FL: Lewis Publications: 47-69.

Hoffman, D.J.; Pattee, O.H.; Wiemeyer, S.N. 1985. Effects of fluoride on Screech Owl reproduction: teratological evaluation, growth, and blood chemistry in hatchlings. Toxicology Letters. 26: 19-24.

James, P.C.; Fox, G.A. 1987. Effects of some insecticides on productivity of Burrowing Owls. Blue Jay. 45: 65-71.

Jones, D.M.; Bennett, D.; Elgar, K.E. 1978. Death of owls traced to insecticide treated timber. Nature. 272: 52.

Karlog, O.; Kraul, I.; Dalgaard-Mikkelsen, S. 1971. Residues of polychlorinated biphenyl (PCB) and organochlorine insecticides in liver tissue from terrestrial Danish predatory birds. Acta Veterinaria Scandinavica. 12: 310-312.

Keith, J.O.; Bruggers, R.L. (in press). Hazards to raptors from pest control in Sahelian Africa. Journal of Raptor Research.

Klaas, E.E.; Swineford, D.M. 1976. Chemical residue content and hatchability of screech owl eggs. Wilson Bulletin. 88: 421-426.

Klaas, E.E.; Wiemeyer, S.N.; Ohlendorf, H.M.; Swineford, D.W. 1978. Organochlorine residues, eggshell thickness, and nest success in Barn Owls from the Chesapeake Bay. Estuaries. 1: 46-53.

Koeman, J.H.; Van Genderen, H. 1966. Some preliminary notes on residues of chlorinated hydrocarbon insecticides in birds and mammals in the Netherlands. Journal of Applied Ecology. 3(Suppl.): 99-106.

Koeman, J.H.; Vink, J.A.J.; de Goeij, J.J.M. 1969. Causes of mortality in birds of prey and owls in the Netherlands in the winter of 1968-1969. Ardea. 57: 67-76.

Lincer, J.L.; Clark, R.J. 1978. Organochlorine residues in raptor eggs in the Cayuga Lake Basin. New York Fish Game Journal. 25: 121-128.

MacDonald, J.W.; Randall, C.J.; Ross, H.M.; Moon, G.M.; Ruthven, A.D. 1983. Lead poisoning in captive birds of prey. Veterinary Record. 113: 65-66.

Marti, C.D. 1992. Barn Owl. No. 1. In: Poole, A.; Stettenheim, P.; Gill, F., eds. The birds of North America. Philadelphia, PA: Academy of Natural Science, and Washington, DC: American Ornithological Union. 15 p.

McLane, M.A.R.; Hall, L.C. 1972. DDE thins Screech Owl eggshells. Bulletin Environmental Contamination and Toxicology. 8: 65-68.

McLane, M.A.R.; Hughes, D.L. 1980. Reproductive success of Screech Owls fed Aroclor 1248. Archives of Environmental Contamination and Toxicology. 9: 661-665.

Mendelssohn, H.; Paz, U. 1977. Mass mortality of birds of prey caused by azodrin, and organophosphorus insecticide. Biology Conservation. 11: 163-170.

Mendenhall, V.M.; Klaas, E.E.; McLane, M.A.R. 1983. Breeding success of Barn Owls (*Tyto alba*) fed low levels of DDE and dieldrin. Archives of Environmental Contamination and Toxicology. 12: 235-240.

Mendenhall, V.M.; Pank, L.F. 1980. Secondary poisoning of owls by anticoagulant rodenticides. Wildlife Society Bulletin. 8: 311-315.

Merson, M.H.; Byers, R.E.; Kaukeinen, D.E. 1984. Residues of the rodenticide brodifacoum in voles and raptors after orchard treatment. Journal of Wildlife Management. 48: 212-216.

National Research Council. 1991. Animals as sentinels of environmental health hazards. Washington, DC: National Academy Press. 160 p.

Newton, I.; Wyllie, I.; Asher, A. 1991. Mortality causes in British Barn Owls *Tyto alba*, with a discussion of aldrin-dieldrin poisoning. Ibis. 133: 162-169.

Newton, I.; Wyllie, I.; Freestone, P. 1990. Rodenticides in British Barn Owls. Environment Pollution. 68: 101-117.

Newton, I.; Wyllie, I.; Gray, A.; Eadsforth, C.V. 1994. The toxicity of the rodenticide flocoumafen and its elimination via pellets. Pesticide Science. 41: 187-193.

Noble, D.G.; Elliott, J.E. 1990. Levels of contaminants in Canadian raptors, 1966 to 1988; effects and temporal trends. Canadian Field-Naturalist. 104: 222-243.

Okoniewski, J.C.; Novesky, E. 1993. Bird poisonings with cyclodienes in suburbia:

links to historic use on turf. Journal of Wildlife Management. 57: 630-639.

Olsen, P.; Fuller, P.; Marples, T.G. 1993. Pesticide-related eggshell thinning in Australian raptors. Emu. 93: 1-11.

Pain, D.J.; Amiard-Triquet, C. 1993. Lead poisoning of raptors in France and elsewhere. Ecotoxicology Environment Safety. 25: 183-192.

Pattee, O.H.; Wiemeyer, S.N.; Swineford, D.M. 1988. Effects of dietary fluoride on reproduction in Eastern Screech-owls. Archives of Environmental Contamination and Toxicology. 17: 213-218.

Peakall, D.B.; Kemp, A.C. 1980. Organochlorine levels in owls in Canada and South Africa. Ostrich. 51: 186-187.

Postupalsky, S. 1970. Effects of pesticides on populations of bald eagle and other fish-eating birds in the Lake Nipigon and Lake Superior region of Ontario. Ottawa, Canada: Canadian Wildlife Service Report. 29 p.

Redig, P.T.; Stowe, C.M.; Arendt, T.D.; Duncan, D.H. 1982. Relay toxicity of strychnine in raptors in relation to a pigeon eradication program. Veterinary and Human Toxicology. 24: 335-336.

Rinsky, A.; Perry, A.S. 1981. Induction of the mixed-function oxidase system in the liver of the Barn Owl *Tyto alba* by PCB's. Pesticide Biochemical Physiology. 16: 72-78.

Seidensticker, J.C., IV; Reynolds, H.V., III. 1971. The nesting, reproductive performance, and chlorinated hydrocarbon residues in the Red-tailed Hawk and Great Horned Owl in south-central Montana. Wilson Bulletin. 83: 408-418.

Sheffield, S.R.; Kendall, R.J. (in press). Wildlife species as sentinels of environmental health hazards. Environment Health Perspective.

Sierra, M.; Santiago, D. 1987. Organochlorine pesticide levels in Barn Owls collected in Leon, Spain. Bulletin Environmental Contamination and Toxicology. 38: 261-265.

Springer, A.S. 1980. Pesticide levels, egg and eggshell parameters of Great Horned Owls. Ohio Journal of Science. 80: 184-187.

Stanley, P.I.; Elliot, G.R. 1976. An assessment based on residues in owls of environmental contamination arising from the use of mercury compounds in British agriculture. Agro-Ecosystems. 2: 223-234.

Steininger, F. 1952. Rodent control and secondary poisoning of birds of prey and owls. Ornithologische Mitteilongen. 4: 36-39.

Stone, W.B.; Okoniewski, J.C. 1983. Organochlorine toxicants in Great Horned Owls from New York, 1981-1982. Northeastern Environmental Science. 2: 1-7.

Stone, W.B.; Okoniewski, J.C. 1988. Organochlorine pesticide-related mortalities of raptors and other birds in New York, 1982-1986. In: Cade, T.J.; Enderson, J.H.; Thelander, C.G.; White, C.M., eds. Peregrine falcon populations: their management and recovery. Boise, ID: The Peregrine Fund: 429-438.

Sundlof, S.F.; Forrester, D.J.; Thompson, N.P.; Collopy, M.W. 1986. Residues of chlorinated hydrocarbons in tissues of raptors in Florida. Journal of Wildlife Disease. 22: 71-82.

Townsend, M.G.; Fletcher, M.R.; Odam, E.M.; Stanley, P.I. 1981. An assessment of the secondary poisoning hazard of warfarin to Tawny Owls. Journal of Wildlife Management. 45: 242-248.

White, C.M. 1994. Population trends and current status of selected western raptors. Studies of Avian Biology. 15: 161-172.

Wiemeyer, S.N. 1991. Effects of environmental contaminants on raptors in the midwest. In: Proceedings, Midwest raptor management symposium workshop. Sci. Tech. Ser. 15. Washington, DC: National Wildlife Federation: 168-181.

Wiemeyer, S.N.; Hill, E.F.; Carpenter, J.W.; Krynitsky, A.J. 1986. Acute oral toxicity of sodium cyanide in birds. Journal of Wildlife Disease. 22: 538-546.

Wiemeyer, S.N.; Hoffman, D.J. 1996. Reproduction in Eastern Screech-owls fed selenium. Journal of Wildlife Management. 60: 332-341.

Wiemeyer, S.N.; Spann, J.N.; Bunck, C.M.; Krynitsky, A.J. 1989. Effects of Kelthane on reproduction of captive Eastern Screech-owls. Environment Toxicology and Chemistry. 8: 903-914.

Wiemeyer, S.N.; Sparling., D.W 1991. Acute toxicity of four anticholinesterase insecticides to American Kestrels, Eastern Screech-owls, and northern bobwhites. Environmental Toxicology and Chemistry. 10: 1139-1148.

Wyllie, I. 1995. Potential secondary poisoning of Barn Owls by rodenticides. Pesticide Outlook. 5: 19-25.

Appendix 1.—*Listing of common and scientific names of owls used in this paper.*

Aegolius acadicus—Northern Saw-whet Owl (AEAC)
Aegolius funereus—Boreal (nearctic) or Tengmalm's (palaearctic) Owl (AEFU)
Asio capensis—Marsh Owl (ASCA)
Asio otus—Long-eared Owl (ASOT)
Asio flammeus—Short-eared Owl (ASFL)
Athene noctua—Little Owl (ATNO)
Bubo africanus—Spotted Eagle Owl (BUAF)
Bubo bubo—Eagle Owl (BUBU)
Bubo bubo bengalensis—Indian Eagle Owl (BBBE)
Bubo capensis—Cape Eagle Owl
Bubo virginianus—Great Horned Owl (BUVI)
Glaucidium passerinum—Pygmy Owl (GLPA)
Glaucidium perlatum—Pearl-spotted Owlet (GLPE)
Ninox rufa—Rufous Owl (NIRU)
Ninox strenua—Powerful Owl (NIST)
Ninox connivens—Barking Owl (NICO)
Ninox novaeseelandiae—Southern Boobook Owl (NINO)
Nyctea scandiaca—Snowy Owl (NYSC)
Otus asio—Eastern Screech-owl (OTAS)
Otus kennicottii—Western Screech-owl (OTKE)
Otus scops—Scops Owl (OTSC)
Strix varia—Barred Owl (STVA)
Strix nebulosa—Great Gray Owl (STNE)
Strix aluco—Tawny Owl (STAL)
Speotyto (Athene) cunicularia—Burrowing Owl (SPCU)
Surnia ulula—Northern Hawk Owl (SUUL)
Tyto alba—Barn Owl (TYAL)
Tyto capensis—Grass Owl (TYCA)
Tyto longimembris—Eastern Grass Owl (TYLO)
Tyto novaehollandiae—Masked Owl (TYNO)
Tyto tenebricosa—Sooty Owl (TYTE)

Current Status, Distribution, and Conservation of the Burrowing Owl (*Speotyto cunicularia*) in Midwestern and Western North America

Steven R. Sheffield[1]

Abstract.—The Burrowing Owl (*Speotyto cunicularia*) inhabits open prairie grassland habitat in the midwestern and western US and Canada. For several years now, numbers of this species in North America have been declining at an alarming rate. Currently, Burrowing Owls are listed as endangered in Canada and threatened in Mexico. In the United States, the Burrowing Owl was listed as a Candidate 2 species by the USFWS until 1996, but currently is not formally a listed species. However, Burrowing Owls are listed as either endangered, threatened, or a species of special concern in virtually every state/province in which it occurs in midwestern and western North America. Habitat destruction/alteration, with a subsequent increase in mammalian predation has played a major role in the decline of populations. Exposure to large amounts of pesticides and other human-related disturbances have also played a role in their decline. Burrowing Owls rely on colonial sciurid towns as an integral part of their preferred habitat, but black-tailed prairie dog (*Cynomys ludovicianus*) populations have been reduced over 98 percent since 1900. These important components of the North American prairie ecosystem are significant and highly coevolved systems where resident species such as Burrowing Owls rely to a significant extent on the other species in the system. I suggest that Burrowing Owls serve as a model sentinel species of the health of the midwestern and western grassland ecosystems and that proactive conservation measures and changes in policy are necessary for the continued existence of populations of Burrowing Owls.

The Burrowing Owl (*Speotyto cunicularia*) is an inhabitant of the prairie grassland ecosystem of midwestern and western North America. This particular ecosystem is considered by many to be at greatest risk of human perturbation. This species has experienced both local and regional population declines and as a result it is listed in virtually all states and provinces in which it occurs. Specifically, the subspecies *S. c. hypugea*, the western Burrowing Owl, is the taxon of Burrowing Owl listed in midwestern and western North America.

The objectives of this paper are to present the current population status, distribution, and conservation status of the Burrowing Owl in midwestern and western North America. In addition, a further objective is to review current conservation measures taken for Burrowing Owls and to suggest future research and conservation needs for this species.

Populational trends presented here are derived from 30 years of Breeding Bird Count (BBS) data (Sauer *et al.* 1996a) and Christmas Bird Count (CBC) data (Sauer *et al.* 1996b). BBS data are from 1966-1994 and CBC data are from 1959-1988. Avian population counts such as the BBS and CBC generally are now acknowledged to be useful indicators of patterns of avian biogeography and population trends. The BBS and CBC data allow analysis of distribution and abundance of avian species during the breeding season (late spring) and during early winter, respectively. In addition, these long-term databases probably are more reliable for the highly diurnal and relatively easy to count Burrowing Owl than for most other raptor species. Although these databases are invaluable as tools to estimate population numbers and trends, there are certain pitfalls associated with their use (see Butcher 1990 and Droege 1990 for details on uses of BBS and CBC data, respectively).

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POPULATION STATUS/DISTRIBUTION

The Burrowing Owl occurs from the southern portions of western Canada through the western United States and Mexico through Central America and into South America south to southern Argentina (Haug *et al.* 1993). Disjunct populations occur in Florida and adjacent Caribbean Islands. In Canada, Burrowing Owls occur in Manitoba, Saskatchewan, Alberta, and British Columbia (fig. 1). In the United States, Burrowing Owls occur from western Minnesota and Iowa to south to Texas and west from Washington through California (fig. 1).

Maps of average count and percent change/year for Burrowing Owls from BBS data are shown in figure 2. The BBS data indicate that there has been an overall decrease of 0.6 percent/year in Burrowing Owl numbers in North America and 0.5 percent/year in the US (table 1). For both North America and the US, however, the trends from 1966-1979 were a 1.6 percent and 1.8 percent increase in numbers and the trend from 1980-1994 was a 2.1 percent and 2.0 percent increase in numbers, respectively. In the Central Region of North America, there was a 2.8 percent/year decrease overall, a 2.3 percent/year increase from 1966-1979 and 0.5 percent/year decrease from 1980-1994 (table 1). In this region, significant recent (from 1966-1979 to 1980-1994) declines were seen in North Dakota, New Mexico, Nebraska, and Texas (table 1). Significant declines over shorter periods of time have been seen in west-central Kansas, adjacent portions of Oklahoma and Nebraska, western portions of the Texas panhandle, the Trans-Pecos region of Texas, and southern New Mexico (Haug *et al.* 1993). Significant increases were seen in Colorado and South Dakota. In the Western Region of North America, there was a 4.6 percent/year increase overall, a 1.3 percent

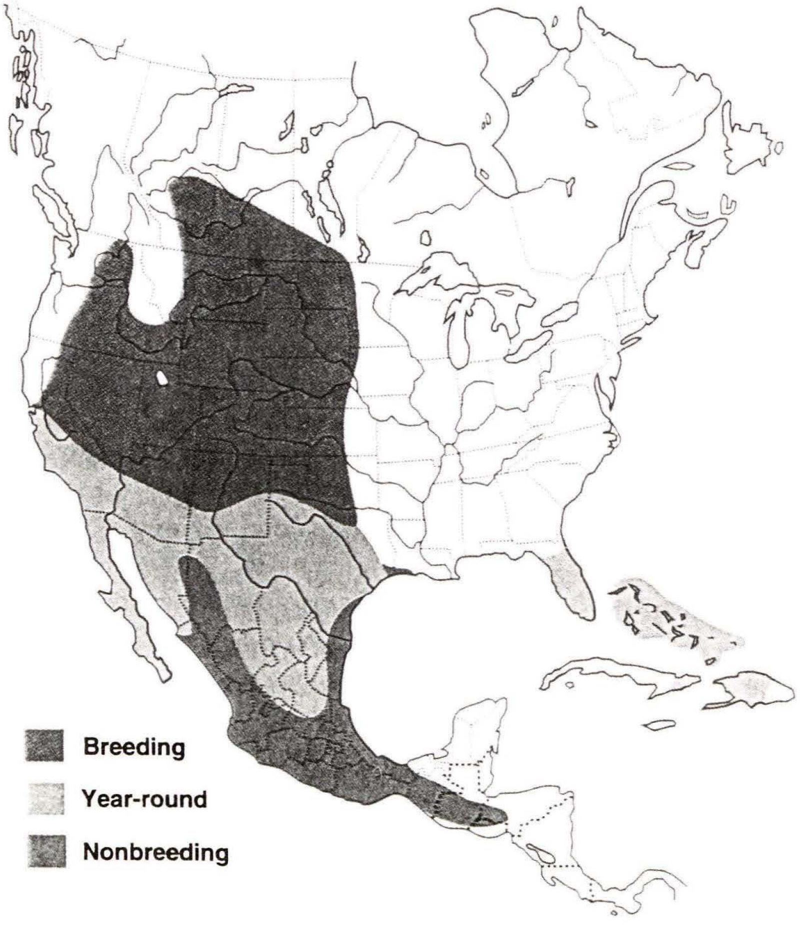

Figure 1.—*Range map of the Burrowing Owl (*Speotyto cunicularia*) in North America (map from Haug* et al. *1993).*

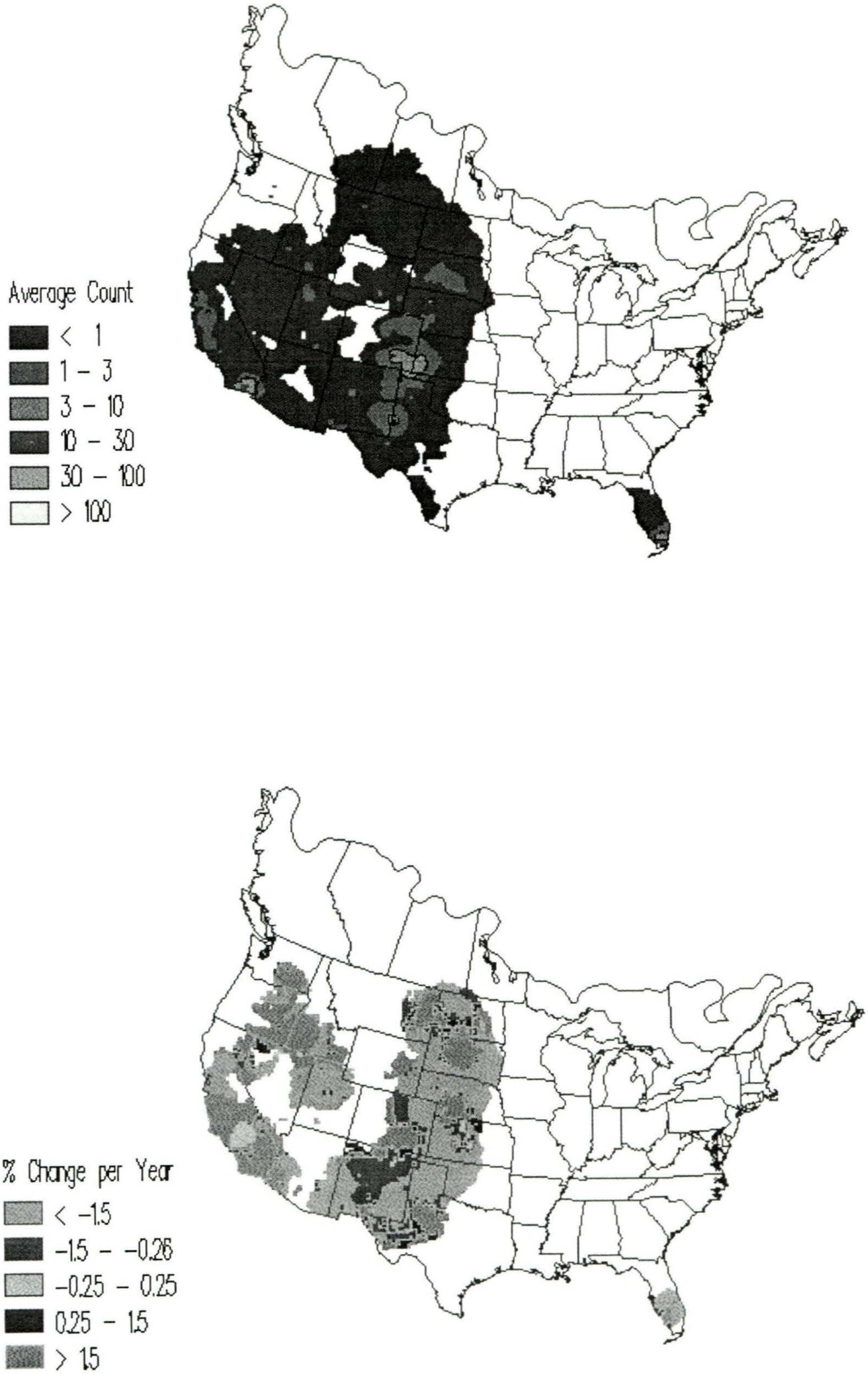
Average Count
< 1
1 - 3
3 - 10
10 - 30
30 - 100
> 100
% Change per Year
< -1.5
-1.5 - -0.26
-0.25 - 0.25
0.25 - 1.5
> 1.5

Figure 2.—*Maps of average count and percent change per year for Burrowing Owls (*Speotyto cunicularia*) from Breeding Bird Survey data (1966-1994; from* Sauer et al. *1996a).*

Table 1.—*Population trend (percent change/year) based on breeding bird survey data for the Burrowing Owl (*Speotyto cunicularia*) in North America (1966-1994) (Sauer* et al. *1996a).*

Area	Population trend (N)		
	(1966-1994)	(1966-1979)	(1980-1994)
North America	-0.6 (245)	+1.6 (121)	+2.1 (175)
United States	-0.5 (238)	+1.8 (116)	+2.0 (173)
Central Region	-2.8 (128)	+2.3 (66)	-0.5 (96)
Western Region	+4.6 (109)*	+1.3 (51)	+4.2 (74)*
California	+5.3 (32)*	-2.3 (20)	+6.3 (22)*
Colorado	-3.8 (25)	-7.1 (9)	+4.7 (23)
Nebraska	+6.0 (15)	+25.5 (8)*	-2.0 (10)
New Mexico	-0.6 (22)	-4.1 (6)*	-1.6 (18)
North Dakota	+4.2 (16)	+11.2 (8)	-9.9 (13)*
South Dakota	-5.8 (19)	+5.6 (15)	+10.1 (9)
Texas	-1.4 (22)	+18.9 (14)	-8.0 (17)

* = significant population trend

increase from 1966-1979 and a 4.2 percent increase from 1980-1994 (table 1). However, data from this region is less complete than that from the Central Region and is made up mainly from California. In this region, significant increases were seen in California. However, it is known that Burrowing Owls were extirpated from British Columbia by 1980 (Haug *et al.* 1993). In California, a survey by DeSante and Ruhlen (1995) has shown that there has been approximately a 50 percent decline in numbers in the State over the last 10 years. However, significant increases over shorter periods of time have been seen in the lower Sonoran Desert, lower Colorado River Valley in western Arizona and adjacent California, and the interior valley of California (Haug *et al.* 1993).

The CBC data are more limited for Burrowing Owls since northern populations move south for the winter. Burrowing Owls are known to winter primarily in California, Arizona, New Mexico, Texas, Louisiana, and Florida (fig. 3). Overall, available data indicate a significant decrease of about 0.6 percent/year (table 2). California showed a significant decreasing trend (1.2 percent/year), while Arizona and Texas showed slight increasing trends (table 2). However, overall CBC data for Burrowing Owls suggest a decline in numbers since the mid-1970's. A similar analysis of Burrowing Owl wintering numbers using CBC data found comparable overall trends in numbers in the United States, although analysis including Florida resulted in a slightly positive overall trend and analysis of the limited CBC data from Mexico indicated that Mexican populations were decreasing slightly as well (James and Ethier 1989).

REASONS FOR DECLINE

It is clear that the number one reason for the overall decline of Burrowing Owls is the destruction and alteration of their habitat. This has come about largely due to development of grasslands into agricultural croplands and through destruction of prairie dog towns. As long ago as the 1930's, it was recognized that intensive cultivation of grasslands and native prairies was the major factor in declining Burrowing Owl populations (Bent 1938). Burrowing Owls strongly prefer open grassland habitat with colonial sciurid populations, and since 1900, black-tailed prairie dog (*Cynomys ludovicianus*) populations have been reduced more than 98 percent. In addition to direct destruction of prairie dog towns, the shooting of prairie dogs and sylvatic plague have decimated prairie dog populations in many areas. The remaining prairie dog towns are generally highly fragmented and suboptimal nesting and foraging habitat. This has led to a scarcity of suitable nesting burrows for Burrowing Owls in many locations, and may reduce chances that unpaired owls will be able to find mates. Habitat destruction and alteration has also led to indirect negative impacts on Burrowing Owls, including an increased frequency of mammalian predators (White 1994). Such mammalian species as coyotes (*Canis latrans*), red foxes (*Vulpes vulpes*), gray foxes (*Urocyon*

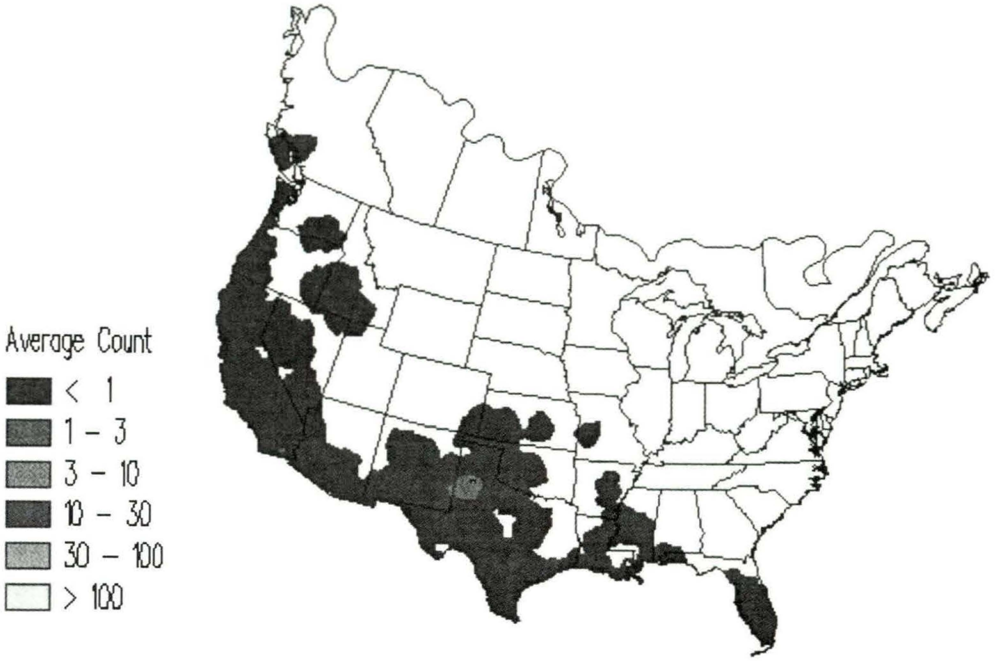

Figure 3.—*Map of winter distribution of Burrowing Owls (*Speotyto cunicularia*) from Christmas Bird Count data (1959-1988; from Sauer* et al. *1996b).*

Table 2.—*Population trend and abundance based on Christmas bird count data for the Burrowing Owl (*Speotyto cunicularia*) in North America (1959-1988; from Sauer* et al. *1996b).*

Area	**Population trend (N)**	**Relative abundance**
North America	-0.6 (213)*	0.12
Arizona	+0.2 (16)	0.10
California	-1.2 (97)*	0.29
Texas	+1.2 (52)	0.23

* = significant population trend

cinereoargenteus), and badgers (*Taxidea taxus*) have increased in numbers in many grassland habitats due to the widespread habitat alteration that has tended to modify habitats into early successional stages.

In addition to habitat destruction and alteration, direct mortality due to vehicle collisions and shootings have been important in population declines in some areas (Haug *et al.* 1993). In western Oklahoma, shooting was responsible for 66 percent of the known mortality (Butts 1973). Exposure to environmental contaminants such as anti-cholinesterase (anti-ChE) insecticides has proven to negatively impact Burrowing Owl populations. For example, the carbamate insecticide carbofuran was found to result in severe reproductive effects in exposed Canadian Burrowing Owls (Fox *et al.* 1989). Anti-coagulant rodenticides (e.g., brodifacoum and other second generation (or super warfarin) compounds) and other types of rodenticides (e.g., strychnine) have been shown to cause mortality in many different owl species, even through the ingestion of as few as one poisoned prey item (Sheffield 1997). Burrowing Owls located in proximity to strychnine-coated grain used to control Richardson's ground squirrels (*Spermophilus richardsonii*) were found to have significantly decreased adult body mass and slightly decreased breeding success as compared to control owls (James *et al.* 1990). Burrowing Owls are known to scavenge dead rodents and other prey items, making them highly susceptible to secondary poisoning by insecticides and rodenticides.

At least two life history traits of the Burrowing Owl act to restrict rapid population recovery following mortalities. Due to their small body size and ground nesting habits, Burrowing

Owls are vulnerable to a large number of mammalian, avian, and reptilian predators. Also, they only produce one brood per year, and will renest only if the first nest is destroyed early in breeding (Haug *et al.* 1993).

CONSERVATION STATUS

Since 1972, the Burrowing Owl has been included on the Blue List, a list intended to provide an early warning of North American bird species undergoing population or range reductions. During the past decade, the Burrowing Owl has been listed as declining (Blue List; Tate 1986), vulnerable (Jeopardy List; USDI 1991), sensitive (Sensitive List; USDI 1992), federal threatened (Canada, COSEWIC, 1979, 1991), federal candidate 2 species (USFWS), and declining (White 1994). The federal candidate 2 species category was officially dropped by the USFWS in late 1996 (published in the 5 December 1996 Federal Register). Currently, the Burrowing Owl has no formal federal listing in the US, but is included on an informal internal list of former C2 candidate species known as "Species of Concern." Burrowing Owls are listed as federally endangered in Canada (COSEWIC 1995), and are listed as endangered in the provinces of Manitoba, Saskatchewan, Alberta, and British Columbia in Canada (table 3). Burrowing Owls are listed as a "Species of Special Concern" in almost all of the midwestern and western states of the United States (table 3). In Mexico, Burrowing Owls were listed as a federally threatened (amenazada) species in 1994 (Secretaria de Desarollo Social de Mexico, 1994). In addition, Burrowing Owls are a CITES Appendix 2 species, which makes it illegal to transport or trade this species (or body parts) across international borders without an appropriate convention export permit.

Table 3.—*Conservation status of the Burrowing Owl (*Speotyto cunicularia*) in North America by country and state/province.*

State/Province	Listing
CANADA	ENDANGERED
Alberta	Red List (Endangered)
British Columbia	Red List (Endangered)
Manitoba	Endangered
Saskatchewan	Red List (Endangered)
UNITED STATES	NO LISTING[1]
Arizona	No listing
California	Species of Special Concern
Colorado	Undetermined
Idaho	Species of Special Concern
Iowa	Endangered
Kansas	Species of Special Concern
Minnesota	Endangered
Montana	Species of Special Concern
Nebraska	Species of Special Concern
New Mexico	No listing[2]
North Dakota	Watch (Species of Special Concern)
Oklahoma	Species of Special Concern
Oregon	Species of Special Concern
South Dakota	Species of Special Concern
Texas	No listing
Utah	Species of Special Concern
Washington	Species of Special Concern
Wyoming	Candidate 2 Species
MEXICO	THREATENED

[1] Included on informal federal list of "Species of Concern"

[2] Included on informal state list of "Species of Special Concern"

CONSERVATION MEASURES

Several innovative approaches have been taken in order to conserve Burrowing Owl populations in the United States and Canada. The use of artificial burrows has allowed the establishment of small Burrowing Owl colonies and allows close study of nest success. Artificial perches have also been used to provide increased hunting and predator observation sites. Pesticide label restrictions now exist for carbofuran use in and around Burrowing Owl nesting areas in Canada. More drastic conservation efforts such as reintroduction programs have been attempted with mixed results in British Columbia, Manitoba, and Minnesota. In Canada, a Burrowing Owl recovery plan and a Canadian Burrowing Owl Recovery Team are in place. In the provinces of Manitoba, Saskatchewan, and Alberta, programs to protect private lands from cultivation and reseeding practices through lease agreements (both voluntary and monetary) have been initiated. Another important conservation effort for the Burrowing Owl is mandatory mitigation of developmental impacts in and around its colonies. Relocations of Burrowing Owls have been attempted in California and Saskatchewan. Finally, public education efforts have been underway in many areas throughout the range of the Burrowing Owl. For example, Operation Burrowing Owl in

Saskatchewan has over 500 members and has acted to protect over 40,000 acres of Burrowing Owl habitat (Haug *et al.* 1993).

CONSERVATION RECOMMENDATIONS

The Burrowing Owl will require human assistance if it is to continue to have healthy populations in North America. Among the conservation needs of this species are the following:

1. A change of philosophy is required towards prairie dog and ground squirrel towns and grasslands in general—they should not be looked at as easily developed, weedy or problem areas but should be actively conserved as an integral part of the prairie grassland ecosystem.

2. Tighter controls should exist over grassland development and disturbances, and mitigation of impacts (direct or indirect) should be mandatory. Protection of prairie dog, ground squirrel, and selected other burrowing mammal populations and their towns as habitat should be an integral part of grassland conservation actions.

3. Continued efforts to control prairie dog and ground squirrel populations in midwestern and western North America are detrimental to Burrowing Owl populations. Pesticide use in these systems should never occur in the vicinity of active Burrowing Owl nests and all pesticide use should be closely monitored for negative impacts on Burrowing Owls.

4. The Burrowing Owl should be included as a formal candidate species in the United States. Further, adding candidate species to the list of species receiving recovery plans and active protection (including protection of habitat) should be part of the Endangered Species Act reauthorization bill in the U.S.

5. The passage of a strong, proactive Endangered Species Act reauthorization bill in the U.S. and a Canadian Endangered Species Act are crucial to Burrowing Owl conservation. In addition, affording legal protection to Burrowing Owls in Mexico is of great importance, and efforts should be made to coordinate Burrowing Owl conservation among North American countries.

6. Further research and population monitoring is necessary, including the following areas:
   a. Continued monitoring of population numbers and trends is critically important. Volunteer data is highly valuable to this effort.
   b. The efficacies of conservation measures currently in use require study to determine what works and what does not work. Currently, there is little quantitative information available on the success of various management strategies.
   c. Further development of effective survey techniques.
   d. Further analysis of migration and fate of migratory individuals is badly needed. In particular, it is not known with any certainty where Burrowing Owls winter in Mexico, Central America, or South America. We need to ascertain whether or not there are environmental problems existing in areas occupied by wintering Burrowing Owls.
   e. Continued monitoring and assessment of the hazard of secondary poisoning from pesticides (insecticides and rodenticides) is necessary.
   f. The impact of increased mammalian predators on nesting success of Burrowing Owls needs to be determined.

CONCLUSIONS

Although listed throughout most of their range in North America, Burrowing Owls continue to undergo mild to relatively severe local and regional population declines. The BBS data indicate an overall decreasing trend in North American Burrowing Owls, whereas the CBC data indicate a slight overall increasing trend in North America, although a significant decrease was seen in California, by far the largest wintering population of Burrowing Owls. Virtually all of the reasons for declines in Burrowing Owl populations still occur throughout most of their range. Habitat destruction and alteration probably account for much of the population decline occurring. Prairie dogs and ground squirrels continue to be actively exterminated in many areas of North America, and prairie grasslands continue to be converted for agriculture and other uses. Habitat alteration may indirectly affect Burrowing Owls through the increase in mammalian nest predators. Vehicle collisions, shooting, and exposure to environmental contaminants may be significant sources of Burrowing Owl mortality in some areas. Many different conservation measures have been attempted in recent years in order to conserve Burrowing Owl populations in North America. Burrowing Owls serve as ideal sentinels of the health of the midwestern and western grassland ecosystem. Proactive conservation measures and changes in land use philosophy and policy are necessary for the continued existence of healthy populations of this species in the grasslands of North America.

ACKNOWLEDGMENTS

I would like to thank Lynne Trulio, Dennis Flath, Bob Murphy, Jim Belthoff, and Troy Wellicome for interesting discussions on Burrowing Owls, Geoff Holroyd for providing some information on conservation statuses of Burrowing Owls, and Paul James for helpful comments on the manuscript.

LITERATURE CITED

Bent, A.C. 1938. Life histories of North American birds of prey. U.S. Nat. Mus. Bull. 170.

Butcher, G.S. 1990. Audubon Christmas bird counts. In: Sauer, J.R.; Droege, S., eds. Survey designs and statistical methods for the estimation of avian population trends. U.S. Fish Wildlife Service, Biology Report. 90(1): 5-13.

Butts, K.O. 1973. Life history and habitat requirements of Burrowing Owls in western Oklahoma. Stillwater, OK: Oklahoma State University. 188 p. M.S. thesis

COSEWIC. 1995. Canadian species at risk. Report of the committee on the status of endangered wildlife in Canada. April 1995. 16 p.

DeSante, D.F.; Ruhlen, E. 1995. A census of Burrowing Owls in California, 1991-1993. Point Reyes Station, CA: Institute for Bird Populations,

Droege, S. 1990. The North American breeding bird survey. In: Sauer, J.R.; Droege, S., eds. Survey designs and statistical methods for the estimation of avian population trends. U.S. Fish Wildlife Service, Biology Report. 90(1): 1-4.

Fox, G.A.; Mineau, P.; Collins, B.; James, P.C. 1989. The impact of the insecticide carbofuran (Furadan 480F) on the Burrowing Owl in Canada. Tech. Rep. Ser. 72. Ottawa, Ontario, Canada: Canadian Wildlife Service.

Haug, E.A.; Millsap, B.A.; Martell, M.S. 1993. Burrowing Owl. In: Poole, A.; Gill, F., eds. Birds of North America, No. 61. Washington, DC: American Ornithological Union, and Philadelphia, PA: Academy of Natural Sciences. 19 p.

James, P.C.; Ethier, T.J. 1989. Trends in the winter distribution and abundance of Burrowing Owls in North America. American Birds. 43: 1224-1225.

James, P.C.; Fox, G.A.; Ethier, T.J. 1990. Is the operational use of strychnine to control ground squirrels detrimental to Burrowing Owls? Journal of Raptor Research. 24: 120-123.

Sauer, J.R.; Hines, J.E.; Gough, G.; Thomas, I. Peterjohn, B.G. 1996a. The North American breeding bird survey results and analysis home page. Version 96.3. Laurel, MD: Patuxent Wildlife Research Center. http: //www.mbr.nbs.gov:80/bbs/.

Sauer, J.R.; Schwartz, S.; Hoover, B. 1996b. The Christmas bird count home page. Version 95.1. Center, Laurel, MD: Patuxent Wildlife Research. http: //www.mbr.nbs.gov/bbs/cbc.html.

Secretaria de Desarollo Social de Mexico. 1994. Que determina las especies y subspecies de flora y fauna silvestres terrestres y aquaticas en peligro de extinction, amenazadas, raras y sujetas a proteccion especial, y que estableces especificationes para su proteccion. Norma Oficial Mexicana NON-059-ECOL-1994. Diario de la Federacion, Mexico, 487: 2-60.

Sheffield, S.R. 1997. Owls as biomonitors of environmental contamination. In: Duncan, J.R.; Johnson, D.H.; Nicholls, T.H., eds. Biology and conservation of owls of the northern hemisphere: 2d international symposium; 1997 February 5-9; Winnipeg, Manitoba. Gen. Tech. Rep. NC-190. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station: 399-408.

Tate, J., Jr. 1986. The blue list for 1986. American Birds. 40: 227-236.

U.S. Department of Interior. 1991. Endangered and threatened wildlife and plants; animal candidate review for listing, proposed rule: Part VIII. Federal Register 56:58804-58836.

U.S. Department of Interior. 1992. Endangered and threatened wildlife and plants. 50 CFR 17.11 & 17.12, 29 Aug. 1992.

White, C.M. 1994. Population trends and current status of selected western raptors. Studies in Avian Biology. 15: 161-172.

Male Eastern Screech-owl (*Otus asio*) Roosting Behavior: Possible Effects from Nesting Stage and Nest Type

Thomas McK. Sproat[1]

Abstract.—This study examined the diurnal roosting behavior of male Eastern Screech-owls (*Otus asio*) and proposed some possible functions for this behavior. As part of a nest defense study, male diurnal roost locations were marked and, later, the distance to the corresponding nest was measured. Male screech-owls roosted significantly closer to their nests during the nestling stage than during the egg stage. Additionally, males associated with nests in natural cavities roosted significantly closer to their nests than did males with nests in nest boxes. Comparison of nest sites showed significantly fewer trees in front of occupied nest boxes, compared to nests in natural cavities. Although the exact function of reducing roost distance is not known, male screech-owls may shift daytime roost locations closer to their nests for anti-predator purposes.

Avian roosting behavior may be influenced by an individual's own risk of depredation (Hayward and Garton 1984) or as a means to reduce heat-stress (Barrows 1981). Under other circumstances, roost site selection may allow owls to better defend or utilize foraging territories. Additionally, owl roost site selection may allow owls to defend against potential nest predators.

Avian nesting success and productivity may be influenced by a parent's ability to defend its eggs or young. Sentinel behavior in the American Crow (*Corvus brachyrhynchos*) has been shown to be a form of parental care in that adults guard the nest against potential predators (D'Agostino *et al.* 1981).

Male Eastern Screech-owls (*Otus asio*) will often perch near or in the nest while the female is brooding the young (Karalus and Eckert 1973). Is this roost-site selection influenced by stage in the nesting cycle or nest type?

METHODS AND MATERIALS

These results are from a post-hoc study taken from an Eastern Screech-owl nest defense study (Sproat 1992). The study was conducted at the Central Kentucky Wildlife Management Area, located 17 km southeast of Richmond, Madison County, Kentucky, USA. The area encompasses about 680 ha and consists of small deciduous woodlots and thickets interspersed with cultivated fields and old fields (see Belthoff 1987).

Screech-owls were captured either by taking them from artificial nest boxes and natural tree cavities or by luring them into mist nets. Owls were fitted with a U.S. Fish and Wildlife Service aluminum leg band and a radio-transmitter (Wildlife Materials Inc., Carbondale, IL). Transmitters were attached backpack style (Smith and Gilbert 1981) with woven nylon cord.

Male daytime roosts were located at 3 to 5 day intervals. Roost trees were marked with aluminum forestry tags and plotted on aerial photos to allow relocation.

Fledgling screech-owls typically left the nest area in mid- to late May, at which time the distances from adult male daytime roosts to the nest tree were measured. In addition, the number of trees within 8 m of each nest tree was recorded. Trees were recorded as either in front of the nest opening (i.e., within 90° of the nest opening) or behind the nest opening. Mean roost distances during two nest stage (egg versus nestling) and two nest types (natural cavity versus nest box) were compared using the Wilcoxon test. The number of trees were compared between nest types using the Mann-Whitney U-test (SAS Institute 1989).

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RESULTS

Of the eight pairs of nesting Eastern Screech-owls monitored, four nested in natural cavities while four others utilized artificial nest boxes. All pairs successfully fledged from one to five nestlings and no mortality was observed in any nest. Male screech-owls roosted significantly closer ($p < 0.001$) to their nest sites during the nestling stage than during the egg stage (nestling = 21.4 ± 3.3 m; egg = 73.1 ± 7.4 m). Male screech-owls associated with natural cavity nest sites roosted significantly closer ($p < 0.01$) to their nests than males associated with nest boxes (cavity = 39.0 ± 5.4 m; nest box = 56.7 ± 5.4 m). Nest boxes used by screech-owls had significantly fewer trees ($P = 0.029$) in front of the nest opening (i.e., within 90° of the nest opening) than natural cavities used for nesting (nest box = 9.8 ± 1.7; cavity = 20.3 ± 3.5). There were no significant differences in the number of trees surrounding nest trees or behind nest trees between nest types (Sproat, unpubl. data).

DISCUSSION

During this study, I observed male Eastern Screech-owls roosting closer to their nests during the nestling stage than during the egg stage. In addition, I documented that males with nests in natural cavities roosted closer than males with nests in nest boxes. There were more trees in front of nests in natural cavities, compared to occupied nest boxes. Several possible explanations may account for these differences.

Roosting closer to the nest during the nestling stage may be related to antipredator nest defense. As the nesting season progresses and vegetation growth provides more cover for potential predators, male screech-owls may reduce their roost distance to better defend their nest. In central Kentucky, screech-owls begin egg-laying in mid- to late March and young typically leave the nest in mid- to late May (Belthoff 1987). During the egg stage of the nesting cycle tree growth is typically dormant and there is no significant understory plant growth. During the nestling stage, trees have leafed out and there is extensive growth of understory vegetation (pers. observ.). Concurrently, as the young grow older they may represent a greater investment to the parents and thus warrant increased defensiveness (Montgomerie and Weatherhead 1988).

Closer roosting by males in natural cavities, compared to their counterparts with nests in artificial nest boxes, may also be a manifestation of antipredator defenses. With more trees in front of natural cavities, males may be able to roost closer to these nests than to nest boxes. Alternatively, the greater number of trees may actually present a greater vulnerability to nest predators and, thus, require greater defensiveness.

The fact that fewer trees were found in front of nest boxes used by nesting screech-owls may be the result of human bias. When placing nest boxes, often at heights over 7 m, biologists may have, inadvertently, selected trees in relatively open areas of the forest. This theory is further supported by the fact that no significant difference was found between nest types in the number of trees either behind or surrounding nest trees. Nest boxes in relatively open areas would be easier to monitor and maintain by biologists but may also influence the roosting behavior of the male screech-owls.

Differences in roost distances may be the result of factors besides antipredator defenses and number of trees near the nest. Male screech-owls may have altered their roost sites in order to reduce their heat stress. As the nesting season progressed and temperatures rose, male owls may have sought cooler roost sites. Alternatively, males may have reduced their roost distance from the nest as a result of increased foraging rate. With the increased demand of feeding nestlings in addition to the brooding female, male screech-owls may have selected closer roost sites as a result of greater foraging activity near the nest. Unfortunately, there were no data from this study regarding either of these hypotheses.

Regardless of the reasons, male Eastern Screech-owls in this study showed distinct differences in their roosting behavior with regard to nest type and stage in the nest cycle. Wildlife personnel should be aware of these factors when making decisions about habitat conservation and nest-site augmentation. While roosting behavior may not significantly influence owl population levels over the short-term, the placement of artificial nest sites may affect owl behavior and thus productivity.

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LITERATURE CITED

Barrows, C.W. 1981. Roost selection by Spotted Owls: an adaptation to heat stress. Condor. 83: 302-309.

Belthoff, J.R. 1987. Post-fledging behavior of the Eastern Screech-owl. Richmond, KY: Eastern Kentucky University. M.S. thesis.

D'Agostino, G.M.; Giovinazzo, L.E.; Eaton, S.W. 1981. The sentinel crow as an extension of parental care. Wilson Bulletin. 93: 394-395.

Hayward, G.D.; Garton, E.O. 1984. Roost habitat selection by three small forest owls. Wilson Bulletin. 96: 690-692.

Karalus, K.E.; Eckert, A.W. 1973. The Owls of North America. New York, NY: Weathervane Books.

Montgomerie, R.D.; Weatherhead, P.J. 1988. Risks and rewards of nest defense by parent birds. Quarterly Review of Biology. 63: 167-187.

SAS Institute. 1989. SAS User's guide: statistics. Cary, NC: SAS Institute.

Smith, D.G.; Gilbert, R. 1981. Backpack radio transmitter attachment success in screech owls (*Otus asio*). North American Bird Bander. 6: 142-143.

Sproat, T. McK. 1992. The nest defense behavior of Eastern Screech-owls. Richmond, KY: Eastern Kentucky University. M.S. thesis.

Auditory Surveys for Northern Saw-whet Owls (*Aegolius acadicus*) in Southern Wisconsin 1986-1996

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Abstract.—During auditory surveys with tape playback between 13 February and 27 April during 1986-1996, our detection of calling by Northern Saw-whet Owls (*Aegolius acadicus*) varied dramatically and regularly in an apparent 4-year cycle: 1986, 1990, and 1994 were significantly high calling years; 1987-1989, 1992-1993, and 1995-1996 were significantly low; and 1991 was intermediate. Calling was also significantly affected positively by increasing time since sunset and negatively by date. Results from daytime searches during 1986-1990 for saw-whet owl individuals, roosts, and pellets did not show annual fluctuation. Three other owl species were also heard during these auditory surveys. Calling by Eastern Screech-owls (*Otus asio*) was not significantly affected by any variable tested. Calling by Great Horned Owls (*Bubo virginianus*) was signicantly affected by annual cycle and year, each with opposite effects than for the saw-whet owl. Calling by Barred Owls (*Strix varia*) showed no year or cycle patterns, but was negatively affected by date and wind, positively affected by increasing cloud cover, and positively correlated with saw-whet owl calling.

Auditory surveys by imitating owl calls or by tape playback have often been used to survey nocturnal owls. Many factors must be considered in designing and interpreting such surveys, including daily and seasonal variability in the species' tendency to vocalize, type of vocalization to use as the stimulus, technical aspects of broadcasting, and harmful effects of broadcasts on the survey species' behavior. Well known problems of such auditory surveying concern both responses to broadcasts and the converse, accommodation (reduced responsiveness) with increasing exposure to the stimulus call, so that moderation in frequency and intensity of broadcasts is advised. To account for individuals known to be present through other means but undetected by auditory surveys, correction factors have been calculated so that local population size can be determined (Fuller and Mosher 1981, Johnson *et al.* 1981).

Auditory surveys of nocturnal owls produce valuable distributional and abundance data, but an understanding of the species' vocal behavior is necessary for proper interpretation. Here we report on inter-year variability in amount of calling by Northern Saw-whet Owls (*Aegolius acadicus*), as well as other factors affecting their vocal responsiveness. We also report statistical analyses of calling by other owl species heard during these auditory surveys.

METHODS

Each year during 1986-1996, we conducted auditory surveys for saw-whet owls in the Baraboo Hills, Sauk County, southwestern Wisconsin, USA (43°23' to 43°34'N, 89°41' to 89°49'W). The westernmost site was Baxter's Hollow, a stream gorge with mixed deciduous-coniferous forest. At the nearest point 5.3 km to the east, the second site was the south shore of Devil's Lake State Park, which has rugged terrain with deciduous and deciduous-coniferous forests plus some open areas. At the nearest point 1.6 km to the north, the third site was Steinke Basin in Devil's Lake State Park, containing wet meadow and grassland with scattered pine plantations and oak-pine forest on the perimeter. These study areas were described in more detail in Swengel and

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Swengel (1987, 1992b). Cannings (1993) mapped these areas within but at the southern edge of the saw-whet owl's year-round range, but noted the limits of its breeding and wintering ranges are not accurately known and likely vary annually.

Listening stations (stops) held constant in location among years were spaced 100 m apart along four set walking routes totaling 9 km in 1986, then 12-14 km in 1987-1996. Two of these routes totaling 7.2 km at Devil's Lake State Park south shore were mapped in Swengel and Swengel (1987). At each station in 1986, then at alternate stations starting part way through the 1987 survey season, we played 20 seconds of taped Northern Saw-whet Owl song (the series of single, short, high-pitched notes repeated at consistent intervals) obtained from "Voices of New World Nightbirds" (ARA Records, Inc.) with a cassette recorder, paused 1 minute to listen, played another 20 seconds of song, and paused again 1 minute to listen. All surveys were conducted by the two of us together and occurred on evenings after sunset with wind <16 km/hr and little or no precipitation. Surveys occurred on at least 3 evenings each year, with the temperature in the first survey period varying from -11 to 15.5°C (mean 0.15°) and in the second from -15 to 24°C (mean 0.9°).

Each station was surveyed once or twice per year at least 2 weeks apart. During the entire study, the first survey period occurred between 13 February and 29 March and the second between 2 March and 27 April (table 1). Within each year, the two survey periods did not overlap, except in 1986 by 1 day. Surveys occurred a bit earlier over the years to avoid the earlier change to daylight savings time (which begins around April 5), to accomodate our daytime schedules. The years varied in how soon and how much of the routes could be surveyed in each period because of weather, time, and health constraints. However many stations we sampled in a year, all were in the same general area and habitat. In 1991, very little surveying was done; the surveying that was done occurred only in prime saw-whet owl habitat immediately along the south shore of Devil's Lake. In all other years, surveys occurred in all sections of the three study sites; saw-whet owls were heard in all these subareas during this study. Ten stations were surveyed every year of the study in the first survey period, including in 1991. Analysis restricted to results from these 10 stations provides a common baseline for evaluating of timing and location possible in this study.

Table 1.—*Span of dates for the first and second survey periods in southern Wisconsin 1986-1996.*

Year	First period	Second period
1986	9.III[1] - 29.III	28.III - 27.IV
1987	5.III - 20.III	27.III - 4.IV
1988	2.III - 16.III	30.III - 11.IV
1989	7.III - 21.III	2.IV - 12.IV
1990	28.II - 21.III	23.III - 3.IV
1991	23.II - 25.II	5.IV
1992	13.II - 16.II	27.III - 4.IV
1993	14.II - 3.III	5.III - 26.III
1994	11.III - 16.III	25.III - 30.III
1995	16.II - 27.II	2.III - 18.III
1996	15.II - 25.II	9.III - 14.III

[1] II = February, III = March, IV = April.

At each station for each owl species heard, we recorded the type and direction of each call made by each contact (vocalizing individual) in three time periods: before first tape playback and during/after each of the two tape playbacks. We listened a few seconds prior to the first tape playback upon our arrival at the station to determine whether an owl was calling prior to turning on the tape recorder. The number of contacts in each time period was then summed for each species at each station. For this analysis, we did not distinguish whether the same or different owl individual(s) were calling in subsequent time periods per station. For example, if the same saw-whet owl individual called continuously throughout all three time periods at a station, or if a different individual called in each time period, we totaled three contacts. Thus, the number of contacts per station is an index for the amount of calling, not the number of owls calling. Indexing auditory results per station rather than the number of owls responsible for the calling has been suggested by other owl researchers (Holmberg 1979).

These calling indices (number of contacts) at each station on each survey date were natural log-transformed to allow parametric tests for statistical significance ($P < 0.05$) with ABstat 7.20 (1994 Anderson-Bell, Parker, Colorado). Significant results associated with independent variables are described here as "effects" in the sense of statistical correlations, not as causal relationships proven by experiment. Analysis of variance (ANOVA) analyzed differences in number of contacts among years with Duncan's post-hoc test. Stepwise multiple linear regression was set to indicate P values up to 0.1, and included these independent variables:

1. *annual variables*: year and cycle model (explained below);
2. *survey* (whether first or second);
3. *date* (Julian date);
4. *circadian cycle* (time since sunset);
5. *weather variables*: percent cloud cover, temperature, wind;
6. *moon* (phase in days);
7. *contact indices for other owl species*: Great Horned Owl (*Bubo virginianus*), Barred Owl (*Strix varia*), Eastern Screech-owl (*Otus asio*), Northern Saw-whet Owl, excluding whichever species is the dependent variable.

Since regression is a type of correlation, the year variable would detect a progressive trend in amount of calling (i.e., a general increase or decrease over the years) but probably not other annual effects (such as an increase or decrease in the middle years of the study). To allow the regression to test for cyclic tendencies, we created two cycle models. The first regression used cycle model 1, which assumed 1 year of high calling followed by 3 low years. The second regression used model 2, which assumed 1 high year, 1 intermediate, then 2 low. Both models were suggested by the survey data during 1986-1991, when it first became apparent that the annual variation in saw-whet owl contacts might be cyclic.

Prior to the statistical testing for this paper, it appeared to us that model 1 fit 1986-1990 better, model 2 1990-1996; hence the testing of two cycle models. These models were intended to test how appropriate it is to group the years of saw-whet owl contacts into classes by amount, with either two classes (high, low) or three classes (high, intermediate, low). As a further test of how much of the variation in those annual indices could be attributed to a cycle model, we conducted a linear regression of the 11 annual means of contacts per station in both survey periods (one mean per year), including only one independent variable, the cycle model.

RESULTS

A total of 329 contacts (as defined in Methods) with Northern Saw-whet Owls occurred at 172 (18 percent) of 979 stations (counting all surveys at all stations) during 1986-1996. A minimum of two different individuals (as determined by spatial separation or overlap of calls, such as applied to spot mapping in Swengel and Swengel 1987) were detected each year except in 1988 and 1996, when only one individual was heard at one station. At 147 (15 percent) stations during 1986-1996, one or more other owl species were heard: Great Horned Owl at 36 (4 percent), Barred Owl at 90 (9 percent), Eastern Screech-owl at 30 (3 percent). We occasionally found Long-eared Owls (*Asio otus*) during diurnal searches for owl pellets and roosts, but never heard them during auditory surveys. It is beyond the scope of this paper to analyze the numbers and locations of each owl species detected in these surveys.

Northern Saw-whet Owl

The mean saw-whet owl calling index (contacts) per listening station exhibited significant, regular inter-year variation (table 2) (Swengel and Swengel 1995). The ANOVA of indices during both survey periods indicated that the means in 1986, 1990, and 1994 were similar and significantly high, 1987-1989 and 1992-1993 and 1995-1996 were similar and significantly low, and 1991 was intermediate (table 2). ANOVAs restricted to indices from the first or second survey periods produced similar patterns, as did the ANOVA further restricted to the *same* ten stations surveyed each year in the first survey (table 2).

In regression, slightly more of the variation in saw-whet owl calling was described by the first regression and by cycle model 1, with 1 high, then 3 low calling years (table 3). In the second regression, year also had a positive effect; i.e., the years of low calling in the 1990s weren't as low as in the 1980s. Next most significant in each regression was a positive effect of increasing time since sunset. In the first regression only, calling also significantly decreased with increasing date.

Table 2.—*Mean ± SD of total Northern Saw-whet Owl* (Aegolius acadicus) *contacts per station (N) each year in both survey periods, the first survey period, the second survey period, and the same ten stations in the first survey period in southern Wisconsin 1986-1996. Within survey sample, means with no similar letters after them are significantly different (ANOVA with Duncan's post-hoc test, P < 0.05). N is the total number of listening stations surveyed within that period; for both periods, it is the sum of stations surveyed in the first and second periods. For each ANOVA, respectively, F values were 32.13, 16.98, 20.14, 10.32; df were 10 and 968 (residual), 10 and 558, 9 and 399, 10 and 99; and P values were 0.0000 for all.*

Year	**Both periods**					**First period**					**Second period**					**Same stations**			
	N	*mean*	±	*SD*		*N*	*mean*	±	*SD*		*N*	*mean*	±	*SD*		*mean*	±	*SD*	
1986	106	0.84	±	1.2	A	82	0.82	±	1.2	B	24	0.92	±	1.1	A	1.5	±	1.4	A
1987	175	0.011	±	0.11	C	106	0.012	±	0.14	D	69	0			B	0			B
1988	63	0.016	±	0.13	C	48	0.021	±	0.14	D	15	0			B	0			B
1989	74	0.027	±	0.16	C	43	0.047	±	0.21	D	31	0			B	0.10	±	0.32	B
1990	113	0.90	±	1.4	A	56	0.89	±	1.7	B	57	0.91	±	1.0	A	0.40	±	0.70	B
1991	16	0.56	±	1.2	B	15	0.60	±	1.2	BC	1	0			-	0.30	±	0.67	B
1992	59	0.085	±	0.28	C	24	0.17	±	0.38	D	35	0.029	±	0.17	B	0.20	±	0.42	B
1993	86	0.058	±	0.28	C	48	0.10	±	0.37	D	38	0			B	0			B
1994	91	0.96	±	1.2	A	49	1.2	±	1.3	A	42	0.67	±	1.0	A	2.2	±	1.3	A
1995	98	0.21	±	0.52	C	49	0.24	±	0.52	CD	49	0.18	±	0.53	B	0.20	±	0.63	B
1996	98	0.020	±	0.20	C	49	0.041	±	0.29	D	49	0			B	0			B

Only in the first regression did survey period have a positive effect, apparently indicating that more calling occurred on a particular date if in the second survey rather than the first. This was not immediately apparent in the field (table 2). In all low and intermediate years (1987-1989, 1991-1993, 1995-1996), we heard relatively more owl calls in the first survey than the second, but relatively few owl calls were heard in those years overall. By contrast, we heard relatively more owl calls in the second survey in 2 (1986, 1990) of the 3 high years. Since those high years represent most of the owl contacts in our sample, they affect the statistics more. The 3 high years are comparable in timing, since the first survey occurred within the same rather narrow span of dates, as did the beginning of the second survey (table 1). No weather variables had significant effects.

Table 3.—*Regression statistics and results for the first and second regressions of total Northern Saw-whet Owl* (Aegolius acadicus) *contacts per station in southern Wisconsin 1986-1996. Significant (P < 0.05) results are boldfaced.*

	First			**Second**		
Statistics	*N*	*r*	*P*	*N*	*r*	*P*
	922	0.5197	**0.0000**	922	0.4687	**0.0000**
Variables	*Step*	*r*	*P*	*Step*	*r*	*P*
Year				2	+0.1243	**0.0000**
Cycle (1)	1	+0.5210	**0.0000**			
Cycle (2)				1	+0.4508	**0.0000**
Survey	4	+0.0950	**0.0196**			
Date	3	-0.1677	**0.0000**			
Time since sunset	2	+0.1239	**0.0000**	3	+0.0961	**0.0013**
Barred Owl	5	+0.0538	0.0582	4	+0.0506	0.0843

The preceding analyses of saw-whet owl calling were all on the basis of contacts at each listening station during each survey. In univariate regressions of the 11 annual indices of saw-whet owl contacts (i.e., the mean contacts per year, as presented in table 2), either cycle model accounted for 80-83 percent of the annual variation, but cycle model 2 (1 high, 1 intermediate, 2 low years of calling) accounted for slightly more (table 4).

Table 4.—*Regression results for Northern Saw-whet Owl* (Aegolius acadicus) *annual vocal index (N = 11) in southern Wisconsin 1986-1996. Significant (P < 0.05) results are boldfaced.*

	r	**P**
Cycle model 1	+0.8936	**0.0002**
Cycle model 2	+0.9116	**0.0000**

Table 5.—*Mean ± SD of total contacts per station (N) each year in both survey periods for Great Horned (*Bubo virginianus*), Eastern Screech- (*Otus asio*), and Barred Owls (*Strix varia*) in southern Wisconsin 1986-1996. Within species, means with no similar letters after them are significantly different (ANOVA with Duncan's post-hoc test, P < 0.05). For each ANOVA, respectively, F values were 2.32, 3.40, 4.83; df were 10 and 968 (residual) for all; and P values were 0.0106, 0.0002, 0.0000.*

Year	N	Great Horned Owl				Eastern Screech-owl				Barred Owl			
		mean	±	*SD*		*mean*	±	*SD*		*mean*	±	*SD*	
1986	106	0.019	±	0.19	B	0.028	±	0.64	B	0.032	±	0.66	AB
1987	175	0.12	±	0.53	A	0.0057	±	0.076	B	0.11	±	0.51	C
1988	63	0.19	±	0.56	A	0.17	±	0.52	A	0.016	±	0.13	C
1989	74	0.081	±	0.36	AB	0.014	±	0.12	B	0.14	±	0.56	BC
1990	113	0.080	±	0.43	AB	0.0088	±	0.094	B	0.062	±	0.31	C
1991	16	0			B	0.063	±	0.25	B	0.13	±	0.34	ABC
1992	59	0.017	±	0.13	AB	0			B	0.34	±	0.82	AB
1993	86	0.093	±	0.48	B	0.035	±	0.18	B	0.047	±	0.26	C
1994	91	0			B	0.055	±	0.27	B	0.19	±	0.55	ABC
1995	98	0.020	±	0.14	B	0.020	±	0.14	B	0.33	±	0.81	A
1996	98	0.020	±	0.14	B	0.092	±	0.38	AB	0.041	±	0.32	C

Other Owl Species

In ANOVA, the three other owl species heard on auditory surveys exhibited no clear patterns of cyclicity (table 5), and Eastern Screech-owl contacts showed no significant effects in regression (multiple r = 0.0588, N = 922, P = 0.0746). But although no strong annual variation in Great Horned Owl calling was apparent in the field, this species had only two significant effects in regression, cycle and year (table 6). Both of these variables had opposite effects than for saw-whet owl, and cycle model 2 fit better than cycle 1. There was a rather strong pattern of higher Great Horned Owl calling in years with less saw-whet owl calling, and the drop in Great Horned Owl calling in more recent years is also apparent (table 6). But our sample of Great Horned Owl calling was too small to test for the two species directly influencing each other's calling. Thus, it is unclear whether and how the annual patterns of Great Horned Owl and saw-whet owl calling might relate to each other, if at all.

Table 6.—*Regression statistics and results of total Great Horned Owl (*Bubo virginianus*) contacts per station in southern Wisconsin. Significant (P < 0.05) results are boldfaced.*

	First			Second		
Statistics	*N*	*r*	*P*	*N*	*r*	*P*
	922	0.1114	**0.0032**	922	0.1146	**0.0023**
Variables	*Step*	*r*	*P*	*Step*	*r*	*P*
Year	1	-0.0919	**0.0053**	1	-0.1016	**0.0025**
Cycle (1)	2	-0.0716	**0.0299**			
Cycle (2)				2	-0.0778	**0.0203**

In regression, Barred Owl contacts had no year or cycle effects, but showed negative date and wind effects, plus positive effects from cloud cover as well as from saw-whet owl contacts (table 7). To elucidate this last significant correlation further, we compared a graph of the mean annual calling indices of Barred Owls (provided in table 5) to those of saw-whet owls (provided in table 2). Years of higher Barred Owl calling appeared to cluster somewhat around years of higher saw-whet owl calling,

Table 7.—*Regression results for total Barred Owl (*Strix varia*) contacts per station; first and second regressions were identical in southern Wisconsin. Significant (P < 0.05) results are boldfaced.*

Regression Statistics	*N*	*r*	*P*
	922	0.1780	**0.0000**
Variables	*Step*	*r*	*P*
Cloud Cover	1	+0.1058	**0.0018**
Northern Saw-whet Owl	2	+0.0868	**0.0077**
Wind	3	-0.0875	**0.0082**
Date	4	-0.0705	**0.0393**

even though Barred Owl contacts did not show significant annual effects (table 7), but saw-whet owls did (table 3). Similarly, a scatterplot of Barred Owl calls by saw-whet owl calls at each listening station in each survey was mildly consistent with this pattern (i.e., the least-squares regression line was weakly positive in slope), indicating a weak positive correlation between Barred Owl and saw-whet owl calling by listening station within a survey. It was not within the scope of this study to test whether a similar habitat preference between these two species might contribute to this correlation.

We could examine further the possibility that Barred Owl calling might affect saw-whet owl calling, or vice versa. The mean amount of saw-whet owl calling at a station heard after the second tape was slightly higher (mean 0.23 saw-whet owl contacts) following previous Barred Owl calling at the same station compared to no Barred Owl calling earlier at the same station (mean 0.17 saw-whet owl contacts). But this minor difference was not significant in a Mann-Whitney U test (P = 0.2096). Likewise, the mean amount of Barred Owl calling after the second tape was higher (mean 0.19 Barred Owl contacts) after previous saw-whet owl calling at the same station compared to no saw-whet owl calling previously at the station (mean 0.089 Barred Owl contacts), but was not significant in a Mann-Whitney U test (P = 0.1856).

DISCUSSION

Of the owl species analyzed, contacts by Northern Saw-whet Owls produced the most significant effects in regression. The saw-whet owl was the target of the surveys and it was heard more frequently than the other species.

Weather conditions were relatively unimportant in explaining variation in owl contacts (we surveyed in conditions with wind at 16 km/h and little or no precipitation)—only Barred Owl calling had significant weather effects (table 7). Smith and McKay (1984) likewise found weather factors relatively unimportant in explaining variation in Christmas Bird Counts of Great Horned, Barred, and Eastern Screech-owls, although increasing temperature did covary somewhat. Smith *et al.* (1987) found little effect of weather conditions on results of auditory surveys for Eastern Screech-owls, although extreme temperatures and wind decreased response frequency. Holmberg (1979) reported little effect of weather on calling by Tengmalm's Owl (*Aegolius funereus funereus*) within minimal prescriptions for weather conditions during surveys that were roughly comparable to ours, and Palmer (1987) found no significant effects of cloud cover, temperature, and wind on vocalization by Boreal Owls (*A. f. richardsoni*) and saw-whet owls. Lunar phase also had no significant or near-significant effects for any species, similar to Palmer's (1987) finding of an apparently slight but non-significant tendency of greater calling by *Aegolius* during the full moon.

Significant effects were primarily ones of timing: daily (time since sunset), seasonal (both date and survey period), and annual (year, cycle model). The positive effect of time since sunset for the saw-whet owl contrasts with Palmer's (1987) report of no detectable change in vocal intensity for *Aegolius* from sunset until after midnight. The only interspecific relationships occurred between Barred and saw-whet owls.

Northern Saw-whet Owl

Much more so than any other owl species heard on the surveys, the saw-whet owl exhibited pronounced and regular variation in vocal response among years. The first cycle model (1 high year, 3 low) appeared to describe this pattern better in the regression based on contacts per station (table 3), but the second cycle model (1 high year, 1 intermediate, 2 low) was slightly more significant in the regression based on mean annual vocal indices (table 4). The exact pattern of this inter-year variation remains unclear. Palmer (1987) also reported a strong variation in the number of saw-whet owls detected on auditory surveys over 5 years, in a pattern consistent with ours but desynchronized by year: 3 low years (1981-1983), 1 high year (1984), 1 low year (1985).

In one regression, number of saw-whet owl contacts positively covaried quite strongly with year, as a second step following cycle model (table 3). An improvement in our ability to hear faint calls and identify unusual vocalizations might explain this positive year effect, at least in part. But we have no evidence that we failed to recognize certain calls during the early years of the study that we succeeded in identifying in later years; in our field notes, we described all sounds heard on the surveys that were plausibly made by an owl, even if we could not identify it. Furthermore, most contacts with saw-whet owls included the song (like our stimulus tape), which we recognized from the beginning of the study. Even if our ability to recognize saw-whet owl vocalizations did improve markedly during the study, this could not fully explain the annual variability, since the positive year effect is secondary to the significant cycle effect.

It is beyond the scope of this paper to analyze saw-whet owl contacts by habitat type, which is certainly important in explaining their distribution (Swengel and Swengel 1987). However, in all years except 1991 (when we did little surveying), all areas of all study sites were surveyed at least once. Although the exact timing and location could certainly influence the number of saw-whet owl contacts, the annual variation in saw-whet owl contacts was so dramatic it cannot be fully accounted for by subtle variation in timing and location of surveys among years.

Annual indices for saw-whet owl abundance in most migrational banding studies also show annual variability with regional desynchrony and apparent periods of 3-5 years in most cases (reviewed in Swengel and Swengel 1995). This annual variability was so pronounced that it could not be fully explained as simply variation in observer effort and weather conditions among years. But these results, as well as our study, were too short in timespan to prove true cyclicity of saw-whet owl indices.

Hatch-year individuals represent a bigger proportion of migrant saw-whet owls captured in fall than would be expected in the population as a whole (reviewed by Johnsgard 1988). Thus, juveniles may tend to migrate more or be more prone to capture during the banding time period than adults. But numbers of juveniles and adults both vary markedly among years in these studies (Duffy and Kerlinger 1992, Evans and Rosenfield 1987, Weir 1983). The juvenile cohort therefore greatly contributes to annual variation in migrant saw-whet owl indices, perhaps a reflection at least in part of differential breeding success as well as the behavioral factors relating to capturability and migration mentioned above. But the juvenile cohort does not account fully for this inter-year variability in saw-whet owl numbers in banding studies. Cyclicity in prey availability appears to drive the regular irruptive behavior of Boreal Owls, including the closely related Tengmalm's Owl (reviewed by Norberg 1987). Since the study region lies near the border between the saw-whet owl's year-round and wintering ranges and this border likely shifts around among years (Cannings 1993), perhaps because of prey conditions as well as weather or demographic factors, variation in size and movements of migrational cohorts could certainly influence annual variation in numbers of saw-whet owls present in our study region during the auditory survey season.

While our nocturnal auditory surveys resulted in great inter-year variation in number of contacts with saw-whet owls, our diurnal searches during 1986-1990 did not. These searches yielded 1,148 saw-whet owl pellets, 623 saw-whet owl roosts, and 17 roosting saw-whet owl individuals in these study areas (Swengel and Swengel 1992a,b). Those daytime observations occurring during the auditory survey season did not indicate any strong patterns of annual variation in owl abundance. These diurnal results can only be used as crude measures of saw-whet owl abundance. However, they did prove presence of saw-whet owl individuals in the study sites during the auditory survey season. In years of high calling (1986, 1990), our diurnal searches were much less efficient and precise at detecting saw-whet owl individuals than calling surveys. This is consistent with the recent discovery of breeding by Boreal Owls well south of previously known range by use of auditory surveys (review in Palmer 1987; Stahlecker and Duncan 1996). However, in the years of low calling (1987-1989), our diurnal seaches detected many more saw-whet owl individuals than the nocturnal auditory surveys. Overall, the variation in number of saw-whet owl individuals present during the survey season was clearly lower than the variation in the amount of saw-whet owl calling.

Our observed variation in vocal response appears to be a function not just of the number of owls present, but also of their behavioral inclination to vocalize. A possible explanation for this is based on the assumption that response to tape playback is an aggressive (or territorial) response. In such a scenario, variation in responsiveness corresponds to variation in levels of defense, which in turn might relate to variation in amount and intensity of breeding effort. Breeding by high-latitude owl species has been documented to vary dramatically as a consequence of prey availability, with both breeding attempts and success declining in years of low prey availability (reviewed by Norberg 1987 and Johnsgard 1988). Holmberg (1979) reported that Tengmalm's Owls vocalized earlier and more often in years of higher prey availability. Palmer (1987) reported that the peak calling year (1984) of both Boreal and saw-whet owls correlated with high prey availability of *Clethrionomys* and *Microtus* but not *Peromyscus*. Hayward *et al.* (1987b) reported that Boreal Owl calling rates vary widely among years, with almost no calling by males in poor prey years. Swengel and Swengel (1995) reviewed the possibility that cyclicity in abundance of saw-whet owl prey might occur nearer to our study region than in their boreal populations, well known to be cyclical.

Conversely, high prey availability might also affect vocal response, assuming it is a sign of territorial defense. In a shorebird, higher prey density within a winter feeding territory led to increased intrusion from conspecifics, so that feeding territory size indirectly declined with increasing prey density because of increased costs in territorial defense (Myers *et al.* 1979). Hayward *et al.* (1987a) reported that home range size of Boreal Owls increased with decreasing prey availability, but found no evidence that the owls defended foraging territories.

We cannot determine how much of our observed annual vocal variation results from differences in the number of individuals present and from differences in calling behavior, but this distinction is of interest in interpreting auditory surveys. Although we cannot demonstrate why saw-whet owl (and Great Horned Owl) calling might vary annually, we hope others will come forward with observations to clarify this phenomenon. In the meantime, caution is indicated in interpreting auditory surveys, because their results reflect not only distribution but also calling behavior. We concur with Palmer (1987) that because the owl populations themselves appear relatively more stable than their calling behavior, auditory surveys should be conducted for at least several consecutive years (preferably a minimum of 4) to assess owl occurrence in an area, to avoid all study years being low calling years.

Other Owl Species

It is not only unclear why the Great Horned Owl showed significant effects of both year and cycle (table 6), but also why this might significantly fit a cycle assuming a 4-year period. In Canadian research, Houston (1987) and Houston and Francis (1995) reported pronounced 10-year cyclicity in Great Horned Owl breeding attempts, breeding success, and juvenile dispersal, coinciding with cyclic variation in prey abundance of snowshoe hares (*Lepus americanus*). It is possible that the correlational year effect relates to this 10-year period, since our study has lasted 11 field seasons.

The mechanism underlying the significant covariance of Barred Owl contacts with saw-whet owl contacts (table 7), and vice versa near-significantly (table 3), is also unclear. Habitat sympatry may largely explain this effect. The saw-whet owl has appeared strongly associated with forest canopy, our subsequent years of field data being consistent with the habitat analysis in Swengel and Swengel (1987). While we have not analyzed Barred Owl contacts by habitat structure, they also appear forest-associated, more so than Eastern Screech-owl contacts previously analyzed (Swengel and Swengel 1987). These preferences regarding habitat structure are consistent with the literature (reviewed in Johnsgard 1988).

It remains possible that a behavioral component contributes to this effect. While the effect was far from significant, the tendency was slight for more calling by one species to follow calling by the other. At the least, this demonstrates that in our surveys, calling by one species did not suppress the calling of another, also found by McGarigal and Fraser (1985). At most, it suggests the possibility that one species' calling stimulates the other's, more so the calling of the saw-whet owl (the smaller species) inciting the Barred Owl. Much more sampling is required to analyze this conclusively. At present, our analysis on this point is statistically weak, since the vast majority of surveys at the listening stations had no contact with the one species before the second playback (no contacts with saw-whet owls at 864 stations; no contacts with Barred Owls at 937). For whatever reason, with multiple linear regression, this interspecific pattern became significant, although the causality of this correlation remains unclear.

ACKNOWLEDGMENTS

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LITERATURE CITED

Cannings, R.J. 1993. Northern Saw-whet Owl (*Aegolius acadicus*). In: Poole, A; Gill, F., eds. The birds of North America, no. 42. Philadelphia, PA: The Academy of Natural Sciences; and Washington, DC: American Ornithologists' Union.

Duffy, K.; Kerlinger, P. 1992. Autumn owl migration at Cape May Point, New Jersey. Wilson Bulletin. 104: 312-320.

Evans, D.L.; Rosenfield, R.N. 1987. Remigial molt in fall migrant Long-eared and Northern Saw-whet Owls. In: Nero, R.W.; Clark, R.J.; Knapton, R.J.; Hamre, R.H., eds. Biology and conservation of northern forest owls: symposium proceedings; 1987 February 3-7; Winnipeg, MB. Gen. Tech. Rep. RM-142. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 209-214.

Fuller, M.R.; Mosher, J.A. 1981. Methods of detecting and counting raptors: a review. Studies in Avian Biology. 6: 235-246.

Hayward, G.D.; Hayward, P.H.; Garton, E.O. 1987a. Movements and home range use by Boreal Owls in central Idaho. In: Nero, R.W.; Clark, R.J.; Knapton, R.J.; Hamre, R.H., eds. Biology and conservation of northern forest owls: symposium proceedings; 1987 February 3-7; Winnipeg, MB. Gen. Tech. Rep. RM-142. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 175-184.

Hayward, G.D.; Hayward, P.H.; Garton, E.O.; Escano, R. 1987b. Revised breeding distribution of the Boreal Owl in the northern Rocky Mountains. Condor. 89: 431-432.

Holmberg, T. 1979. Punkttaxering av pärluggla *Aegolius funereus* – en metödstudie. Vår Fågelvärld. 38: 237- 244.

Houston, C.S. 1987. Nearly synchronous cycles of the Great Horned Owl and snowshoe hare in Saskatchewan. In: Nero, R.W.; Clark, R.J.; Knapton, R.J.; Hamre, R.H., eds. Biology and conservation of northern forest owls: symposium proceedings; 1987 February 3-7; Winnipeg, MB. Gen. Tech. Rep. RM-142. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 56-58.

Houston, C.S.; Francis, C.M. 1995. Survival of Great Horned Owls in relation to the snowshoe hare cycle. Auk. 112: 44-59.

Johnsgard, P.A. 1988. North American Owls: biology and natural history. Washington, DC: Smithsonian Institution Press. 295 p.

Johnson, R.R.; Brown, B.T.; Haight, L.T.; Simpson, J.M. 1981. Playback recordings as a special avian censusing technique. Studies in Avian Biology. 6: 68-75.

McGarigal, K.; Fraser, J.D.1985. Barred Owl responses to recorded vocalizations. Condor. 87: 552-553.

Myers, J.P.; Connors, P.G.; Pitelka, F.A. 1979. Territory size in wintering Sanderlings: the effects of prey abundance and intruder density. Auk. 96: 551-561.

Norberg, R.Å. 1987. Evolution, structure, and ecology of northern forest owls (keynote address). In: Nero, R.W.; Clark, R.J.; Knapton, R.J.; Hamre, R.H., eds. Biology and conservation of northern forest owls: symposium proceedings; 1987 February 3-7; Winnipeg, MB. Gen. Tech. Rep. RM-142. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 9-43.

Palmer, D.A. 1987. Annual, seasonal, and nightly variation in calling activity of Boreal and Northern Saw-whet Owls. In: Nero, R.W.; Clark, R.J.; Knapton, R.J.; Hamre, R.H., eds. Biology and conservation of northern forest owls: symposium proceedings; 1987 February 3-7; Winnipeg, MB. Gen. Tech. Rep. RM-142. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 162-168.

Smith, D.G.; Devine, A.; Walsh, D. 1987. Censusing screech owls in southern Connecticut. In: Nero, R.W.; Clark, R.J.; Knapton, R.J.; Hamre, R.H., eds. Biology and conservation of northern forest owls: symposium proceedings; 1987 February 3-7; Winnipeg, MB. Gen. Tech. Rep. RM-142. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 255-267.

Smith, D.G.; McKay, B. 1984. The effects of weather and effort on Christmas Bird Counts of owls in Connecticut. American Birds. 38: 383-387.

Stahlecker, D.W.; Duncan, R.B. 1996. The Boreal Owl at the southern terminus of the Rocky Mountains: undocumented longtime resident or recent arrival? Condor. 98: 153-161.

Swengel, S.R.; Swengel, A.B. 1987. Study of a Northern Saw-whet Owl population in Sauk County, Wisconsin. In: Nero, R.W.; Clark, R.J.; Knapton, R.J.; Hamre, R.H., eds. Biology and conservation of northern forest owls: symposium proceedings; 1987 February 3-7; Winnipeg, MB. Gen. Tech. Rep. RM-142. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 199-203.

Swengel, S.R.; Swengel, A.B. 1992a. Diet of Northern Saw-whet Owls in southern Wisconsin. Condor. 94: 707-711.

Swengel, S.R.; Swengel, A.B. 1992b. Roosts of Northern Saw-whet Owls in southern Wisconsin. Condor. 94: 699-706.

Swengel, A.B.; Swengel, S.R. 1995. Possible four-year cycle in amount of calling by Northern Saw-whet Owls. Passenger Pigeon. 57: 149-155.

Weir, R. 1983. Northern Saw-whet Owl studies. Ontario Bird Banding. 16(3): 8-9.

Owl Broadcast Surveys in the Foothills Model Forest, Alberta, Canada

D. Lisa Takats and Geoffrey L. Holroyd[1]

Abstract.—Broadcast surveys are used to determine the presence and relative abundance of nocturnal owls, but there has been little effort to standardize such surveys. This paper examines broadcast survey data collected in 1995 and 1996 in the Foothills Model Forest, Alberta, Canada. Three hundred calls from six species of owls were recorded at 893 stops for a call rate of 0.34 calls per stop. Moon phase significantly affected the rate of owls calls. Owl call rate was significantly lower in the middle of the night (midnight to 3:59) compared to the early night (20:00 to 23:59) and early morning (4:00 to 7:59). During precipitation and strong wind, fewer owls called spontaneously or responded to the playback calls. Call rate of owls also declined with temperature. Owls called significantly more frequently during the 2 minute listening period beginning each 15 minute survey period than in subsequent listening periods after playback. Four behavioral responses to playback were recorded: calling and approaching, silently approaching and calling, silently approaching and not calling, and calling but not approaching.

To effectively manage wildlife, knowledge of distribution, relative abundance and, if possible, density of the wildlife population is important (Mosher and Fuller 1996). In the past few decades raptors have become important in research and conservation (Newton 1979). Raptors are difficult to study in the field because they occur at low densities in most areas, tend to have large home ranges, are extremely mobile, often inhabit remote inaccessible areas, and can be secretive (Craighead and Craighead 1969, Pendleton *et al.* 1987). Owls are even more difficult to study than other raptors because of their nocturnal habits and their propensity to nest in inconspicuous places (McGarigal and Fraser 1985). Pendleton *et al.* (1987) describe a number of techniques for surveying owls: road surveys, foot surveys, aerial surveys, boat surveys, and broadcast surveys.

Broadcast surveys are one of the most widely used techniques to locate and census owls (Fuller and Mosher 1981, Johnson *et al.* 1981, Smith 1987). Owls vocalize to communicate with their mates, to delineate territory, and to signal its occupancy (Nicholls and Fuller 1987). They aggressively establish, maintain, and protect their spatial relationships (Gill 1990). Imitating or broadcasting tape recordings of owl vocalizations can invoke vocal responses and many species of owls approach the broadcast source (Fuller and Mosher 1981). Broadcasts can also be utilized to help locate nesting pairs (Devereux and Mosher 1984). This survey technique is usually used in forested areas where owls are difficult to detect. Call rates vary among owl species but can be as high as 82.4 percent as seen in the Barred Owl (*Strix varia*) (Bosa-kowski 1987). Wind velocity, precipitation, and temperature can directly affect owl call counts (Fuller and Mosher 1987).

This paper describes the species and abundance of owls in the Foothills Model Forest (FMF), and evaluates some of the environmental conditions that affect call rates in owls. The results were used to suggest some standard methods for running broadcast surveys.

METHODS

Study Area

The FMF is located in west-central Alberta, Canada, surrounding the town of Hinton, and includes the Weldwood of Canada Forest Management Area, William A. Switzer Provincial Park, the Cache-Percotte Forest, and Jasper National Park (fig. 1). Lodgepole pine (*Pinus contorta*) dominates the landscape throughout the Foothills Natural Region of the FMF. Engelmann spruce (*Picea engelmanii*), and Douglas fir (*Pseudotsuga menziesii*) dominate the Montane Ecoregion. Trembling aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), white spruce (*Picea glauca*), black spruce (*Picea mariana*), and balsam fir (*Abies balsamea*) are common to occasional in both ecoregions. The forest age ranges from young to old and occur in continuous to fragmented stands. The total area of the FMF is 2.3 million hectares.

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Transects

Ten transects (16 km long) were randomly located along roads within 80 km of Hinton in 1995 (Eberhardt and Thomas 1991). In 1996, nine additional transects were set non-randomly (variable lengths), to cover more area and to include Jasper National Park. These transects ensured that a range of habitats were sampled (Van Horne 1983) and large areas were covered efficiently (Fuller and Mosher 1987). Transects were separated by at least 5 km and were spaced far enough apart so that calls could not be heard on more than one transect (Anderson *et al.* 1979). Equally spaced broadcast stations were set along these transects at 1.6 km intervals. Roads had to be accessible in winter and could not have major log hauling on them (safety of the researcher and detectability of owls).

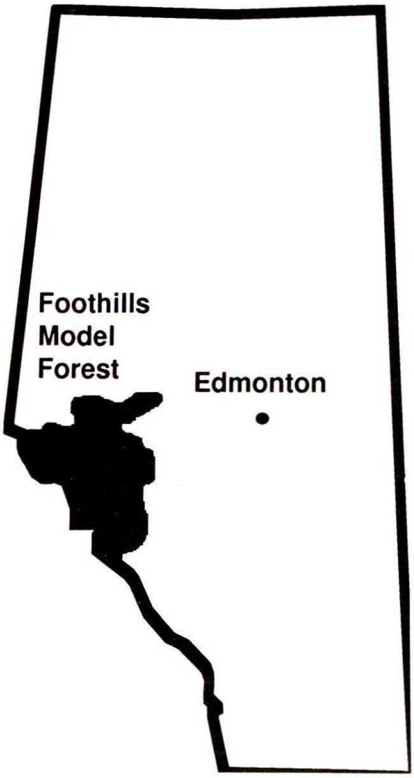

Figure 1.—*Map showing the location of the Foothills Model Forest in Alberta, Canada.*

Broadcast Surveys

Broadcast surveys were conducted during the owls' breeding season (March through May, 1995 and 1996) because call rate during the breeding season is significantly higher than in the non-breeding season (Bosakowski 1987). Transects were completed four times in 1995 and three times in 1996. We looked at the 1995 data and determined that only one survey per month was needed. Only two additional owls were recorded with the fourth survey. A Sony Mega Bass Sports cassette player was used at half volume. This volume was chosen because it could not be heard at a distance of more than 600 m (by the human ear). The cassette player was slowly and continuously rotated 360° during each broadcast, to ensure the sound traveled in all directions. All stops began with a 2 minute listening period and ended with a 5 minute listening period. On the first 10 transects only Barred Owl taped calls were played (fig. 2). The 2 minute silent listening period was followed by a series of six 20-second barred owls broadcasts with 1 minute

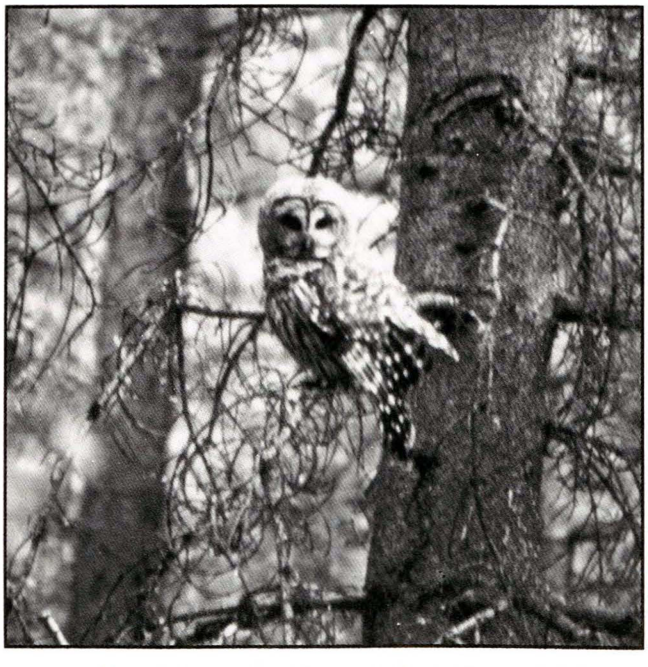
Stephen Glendinning

Figure 2.—*Photo of a Barred Owl (*Strix varia*) Foothills Model Forest, Alberta.*

Table 1.—*Beaufort scale wind speed translations.*

Beaufort number	Wind speed in miles/hr	Indicators of wind speed
0	Less than 1	Smoke rises vertically
1	1 to 3	Wind direction shown by smoke drift
2	4 to 7	Wind felt on face, leaves rustle
3	8 to 12	Leaves, small twigs in motion
4	13 to 18	Raises dust and loose paper; small branches move
5	19 to 24	Small trees sway; crested waves on inland waters

silent listening periods after each broadcast. The total survey time was 15 minutes for each station. If a call could not be identified in the 15 minutes, an additional 10 minutes of listening was added. On the second set of transects broadcasts of three different owl calls, were played in sequence, twice each: Barred Owl, Boreal Owl (*Aegolius funereus*), and Great Gray Owl (*Strix nebulosa*).

The sequence of conducting transects were determined randomly during three time periods, 20:00 to 23:59, 0:00 to 3:59, and 4:00 to 7:59. Counts were not usually conducted in inclement weather (heavy precipitation or strong wind), although if inclement weather started during the latter part of a survey route, the route was completed. Environmental conditions recorded at each stop included: time, start time, temperature (°C), wind speed (Beaufort scale, used in Breeding Bird Surveys, see table 1), precipitation (type and intensity), cloud cover (percent), moon phase (based on the calendar-new moon and eight quarters), moon visible or not at each station, and snow thickness (centimeters). All owl calls were recorded as follows: time of call, broadcast interval (eight intervals), owl species, direction and distance from the observer, and behavior type. Behavior types included: singing and not approaching, singing and approaching, silently approaching and singing, and silently approaching with no vocalization (Beck and Beck, 1988). A sample field data sheet is included (Appendix A).

All data was entered into Microsoft Excel, and then imported into an SPSS (Statistical Package for the Social Sciences) for Windows (1996). Logistic regression was performed on the variables moon phase, moon visible, and night time interval, cloud cover, and temperature, to test their effects on owl call rates. A logistic regression with a covariate was performed to test for interaction between moon phase and cloud cover. Call rates were compared for precipitation and wind events. A comparison was made of the number of owls responding at different broadcast intervals, and the types of behavioral responses.

RESULTS

Calls

A total of 893 stop-counts were completed during March, April, and May, 1995 and 1996. Six species of owls were recorded on the transect surveys (table 2): Barred Owl, Boreal Owl, Great Gray Owl, Great Horned Owl (*Bubo virginianus*), Northern Saw-whet Owl (*Aegolius acadicus*) and Northern Pygmy Owl (*Glaucidium gnoma*). A total of 300 calls from owls were recorded on the transect surveys, a 0.34 call rate. The Boreal Owl was the most abundant owl recorded on transects. Some transects had very few owls recorded on them, possibly due to poor habitat along the transect. The locations of calling owls were recorded on maps to determine the total number of territorial owls (fig. 4).

During 1996, we recorded 87 calls on the first 10 transects (0.29 call rate), and 34 on the nine other ones (0.22 call rate), therefore using the Great Gray Owl and Boreal Owl in addition to the Barred Owl call did not increase over all call rate. Test surveys were conducted in an area with Boreal Owls, to determine if they responded to Barred Owl calls. When a Barred Owl call was played, Boreal Owls responded; when a Boreal Owl call was played, the Boreal Owls stopped calling in some instances (unpubl. data).

Results from all transects were combined to test the effect of environmental conditions on owl call rates. Time of year affected the number of owl calls detected, but this varied by species. The number of calls we recorded were:

Table 2.—*Broadcast survey results, Foothills Model Forest, Alberta, Canada, showing the total number of calls from all species of owls.*

Owl species[1]→	**BAOW**		**BOOW**		**GGOW**		**GHOW**		**NSOW**		**NPOW**	
TRANSECT↓	**1995**	**1996**	**1995**	**1996**	**1995**	**1996**	**1995**	**1996**	**1995**	**1996**	**1995**	**1996**
Gregg Lake	8	8	7	1	0	1	4	5	2	0	0	0
Cold Creek	4	1	25	4	0	2	2	1	0	1	0	0
TriCreeks	2	1	6	0	0	0	4	4	5	2	1	0
Fish Creek	0	0	16	4	0	0	1	3	2	0	0	0
Pedley Road	1	1	3	0	1	1	3	2	4	1	0	0
WildHay Road	4	2	3	1	0	0	1	0	3	1	0	0
Medicine Lodge	1	0	15	9	1	0	2	8	0	6	0	0
Blackcat Ranch	10	6	4	0	0	0	2	0	1	3	0	0
Prest Creek	2	0	4	1	0	0	4	0	3	2	1	0
Lynx Creek	1	2	7	3	0	0	2	0	7	0	0	0
Semi-total	**33**	**21**	**90**	**23**	**2**	**4**	**25**	**23**	**27**	**16**	**2**	**0**
Paul's Road	-	0	-	4	-	0	-	0	-	1	-	0
Beaver	-	0	-	1	-	0	-	0	-	0	-	0
Mercoal	-	0	-	0	-	0	-	6	-	0	-	0
Cache Percotte	-	1	-	1	-	2	-	0	-	0	-	0
Q-road	-	0	-	0	-	0	-	1	-	0	-	0
Snaring	-	0	-	1	-	0	-	0	-	1	-	0
HW 93A/Pyramid	-	3	-	4	-	0	-	0	-	1	-	0
HW 93	-	0	-	1	-	0	-	0	-	1	-	1
Maligne	-	0	-	3	-	0	-	0	-	0	-	1
Semi-total	**-**	**4**	**-**	**15**	**-**	**2**	**-**	**7**	**-**	**4**	**-**	**2**
TOTAL	**33**	**25**	**90**	**38**	**2**	**6**	**25**	**30**	**27**	**20**	**2**	**2**
TOTAL (1995&1996)	**58**		**128**		**8**		**55**		**47**		**4**	

[1] BAOW - Barred Owl (*Strix varia*), BOOW - Boreal Owl (*Aegolius funereus*), GGOW - Great Gray Owl (*Strix nebulosa*), GHOW - Great Horned Owl (*Bubo virginianus*), NSWO - Northern Saw-whet Owl (*Aegolius acadicus*), NPOW - Northern Pygmy Owl (*Glaucidium gnoma*).

83 in March (28 percent), 118 in April (39 percent), and 99 in May (33 percent) (table 3).

Owl call rates varied significantly (Logistic regression, p = 0.0064) between time intervals (fig. 5). Intervals 1 and 3 had higher call rates than Interval 2. Barred Owls, however, had equal call rates in the three time intervals. More owls called in the 2 minute silent period before the first broadcast than in any subsequent 2 minute period (43.7 percent). By the end of the fourth broadcast, most of the calls had occurred (88.7 percent) (fig. 6). Only 10 of the 58 Barred Owls that called were recorded in the first 2 minutes. Owls responded to the broadcasts in a variety of ways (fig. 7). Most of the owls (79 percent) called from a distance, but did not approach the researcher. On 19 percent of the occasions, owls called and then

Lisa Takats

Figure 3.—*Photo of a Great Gray Owl (*Strix nebulosa*), an owl that apparently did not respond well to broadcasts, Foothills Model Forest, Alberta, Canada.*

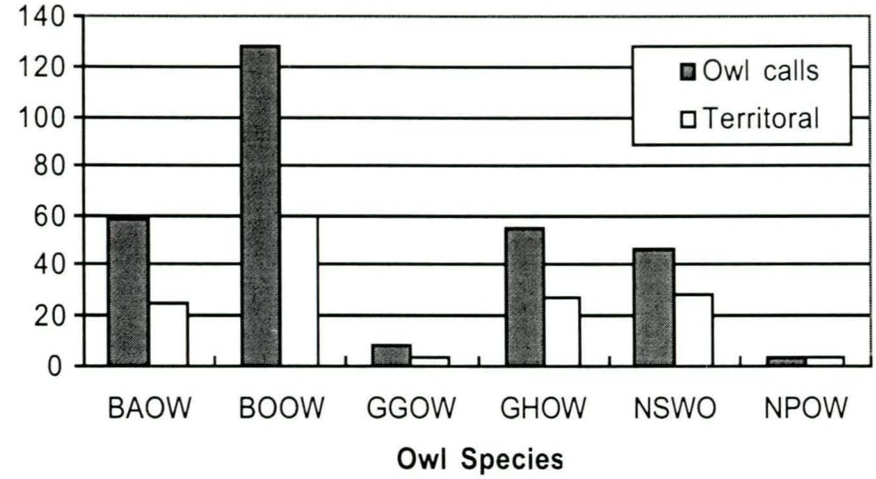

Figure 4.—*Graph showing total number of calls and total number of territorial owls recorded, Foothills Model Forest, Alberta, Canada. Abbreviations are:* BAOW - Barred Owl (*Strix varia*), BOOW - Boreal Owl (*Aegolius funereus*), GGOW - Great Gray Owl (*Strix nebulosa*), GHOW - Great Horned Owl (*Bubo virginianus*), NSWO - Northern Saw-whet Owl (*Aegolius acadicus*), NPOW - Northern Pygmy Owl (*Glaucidium gnoma*).

Table 3.—*Number of owl calls recorded during each month, Foothills Model Forest, Alberta, Canada, 1995 and 1996.*

	March		April		May	
Species[1]	**1995**	**1996**	**1995**	**1996**	**1995**	**1996**
Barred Owl	6	7	11	12	16	6
Boreal Owl	39	7	30	18	22	12
Great Gray Owl	0	1	0	4	2	1
Great Horned Owl	9	6	8	18	8	6
Northern Saw-whet Owl	5	2	5	12	17	6
Northern Pygmy Owl	1	0	0	0	1	2
Total	60	23	54	64	66	33
Month Totals	83		118		99	

[1] Barred Owl (*Strix varia*), Boreal Owl (*Aegolius funereus*), Great Gray Owl (*Strix nebulosa*), Great Horned Owl (*Bubo virginianus*), Northern Saw-whet Owl (*Aegolius acadicus*), Northern Pygmy Owl (*Glaucidium gnoma*).

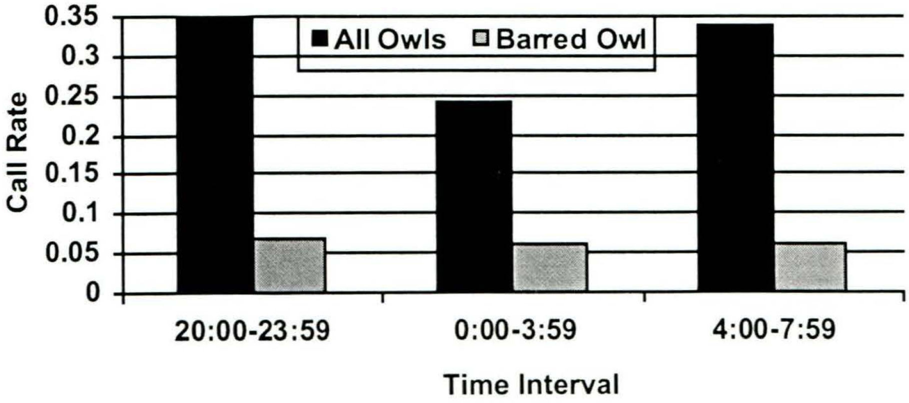

Figure 5.—*Call rate of all owls and Barred Owls* (Strix varia) *at the different time intervals, Foothills Model Forest, Alberta, Canada.*

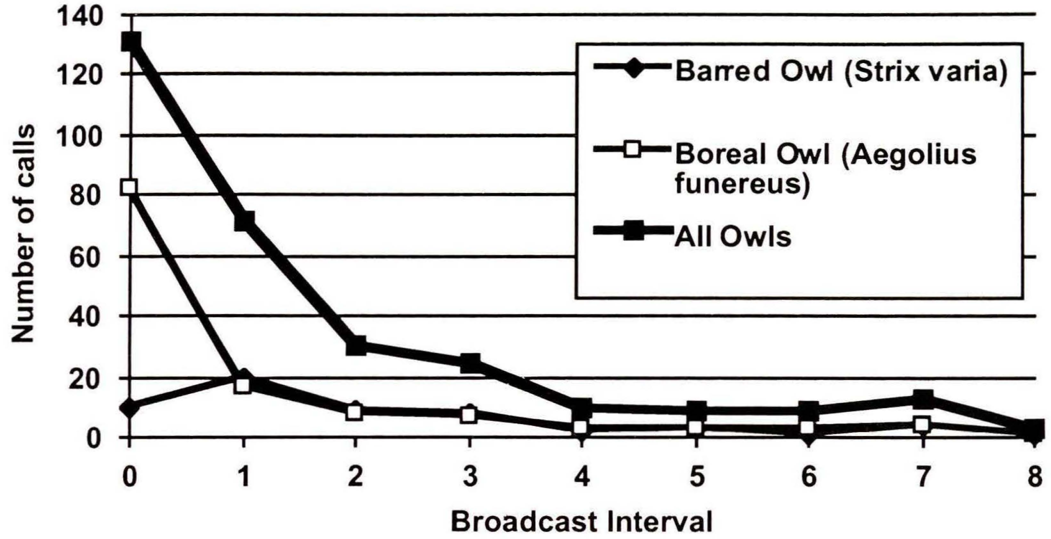

Figure 6.—*Number of owls responding at different broadcast intervals (0 = 2 minute silent period, 1 = after first broadcast, 2 = after second broadcast, etc., 7 = 5 minute listening, 8 = 10 minute listening), Foothills Model Forest, Alberta, Canada.*

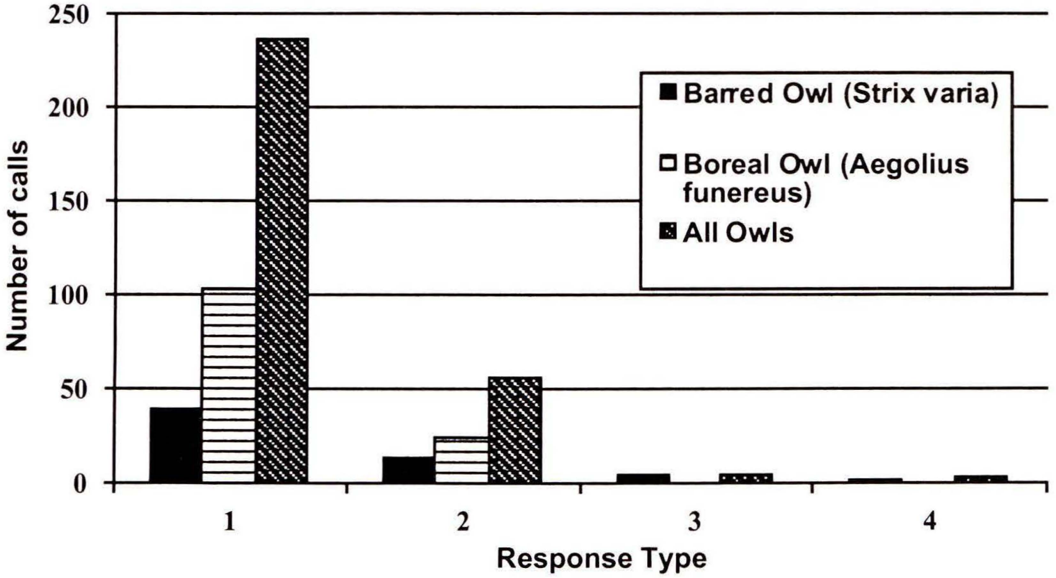

Figure 7.—*Owl responses to broadcast surveys (1 = sings, does not approach; 2 = sings, approaches; 3 = silently approached, sings; 4 = silently approaches, no vocalization), Foothills Model Forest, Alberta, Canada.*

approached. Few owls were detected approaching silently.

Calls and sounds were recorded from 16 other species including: wolves (*Canis lupus*), coyotes (*Canis latrans*), wood frogs (*Rana sylvatica*), boreal chorus frogs (*Pseudacris triseriata*), Common Snipe (*Gallinago gallinago*), Common Nighthawk (*Chordeiles minor*), Common Loon (*Gavia immer*), and various waterfowl species. Three other species of owls were recorded in the FMF, but not during broadcast surveys: Snowy Owl (*Nyctea scandiaca*), Northern Hawk Owl (*Surnia ulula*), and Short-eared Owl (*Asio flammeus*).

Environmental Conditions

The moon phase had a significant effect on owl call (Logistic regression, $p = 0.0025$). Call rates were highest during full moon phase and lowest during new moon phase. Cloud cover did not have a significant effect on call rate (Logistic regression, $p = 0.5276$). When moon phase and cloud cover were tested together as covariates, they significantly affected call rates (Logistic regression, $p = 0.0249$). Therefore, the number of calls increased significantly when the moon was visible.

Owl broadcast surveys were conducted at temperatures ranging from -30°C to +10°C (fig. 8). Owls responded at temperatures as low as -28°C. The rate of calling increased with temperature, and was highest between -15°C and +5°C. Owl call rate dropped as wind speed increased (fig. 9). No owls were recorded when winds exceeded Beaufort scale 4 (over 13 miles/hr). Although most of the transects were not run during precipitation, there were stops where precipitation was recorded. No owls responded during heavy precipitation (fig. 10). Light snow had little effect on owl call rate, however moderate rain and snow did significantly decrease call rate. No owls were recorded during heavy precipitation events.

DISCUSSION

The survey methods described appear to be useful to estimate the distribution and relative abundance of owls. They may be less useful in determining the abundance of Great Gray Owls and Northern Pygmy Owls (figs. 3 and 4), which were also recorded during daytime (unpubl. data).

Environmental conditions directly affect owl calls in a number of ways. Owls called less frequently during heavy precipitation and high wind. Wind can directly affect the researcher's ability to hear owls calling and the owls' ability to hear the broadcast. McGarigal and Fraser (1985) suggest that stops for Barred Owls should last a minimum of 15 minutes. Most of the owl calls in this study were recorded within

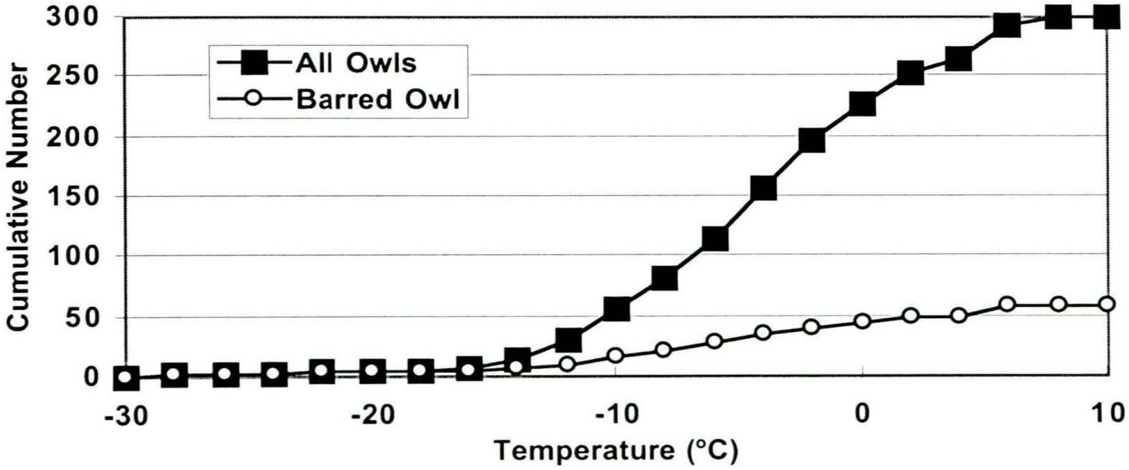

Figure 8.—*Cumulative number of owl calls and Barred Owl* (Strix varia) *calls at increasing temperatures, Foothills Model Forest. Alberta, Canada.*

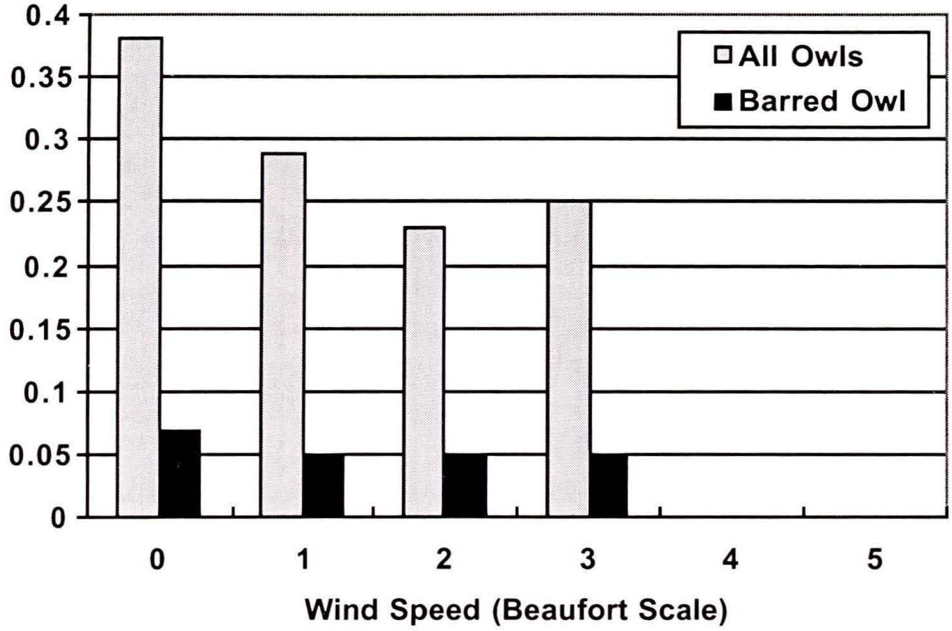

Figure 9.—*Call rate of all owls and Barred Owls (*Strix varia*) at different wind speeds, Foothills Model Forest, Alberta, Canada.*

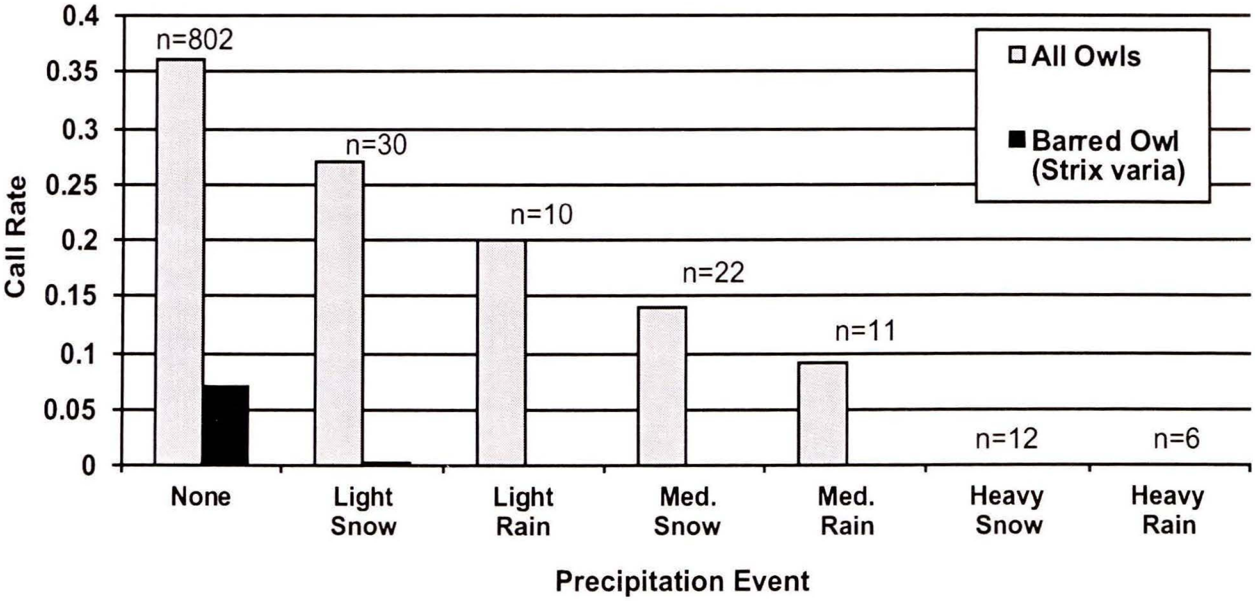

Figure 10.—*Call rates of owls in various amounts of precipitation, n = the number of stops surveyed, Foothills Model Forest, Alberta, Canada.*

7 minutes, suggesting that stops can be shorter. Many owls were calling spontaneously at stations. Only Barred Owls showed an increase in call rate after the first broadcast was played. Owls did not respond more when other species of owl calls were used during the surveys. Barred Owl vocalizations can elicit calls from most species of owls in the Foothills Model Forest Study Area, Alberta. Survey transects are an excellent way to survey large areas efficiently.

Suggestions for Standardized Surveys

1. A silent listening period of at least 2 minutes, before broadcasts, is recommended.
2. Run surveys before midnight and after 4:00 in the morning to get the highest call rates.
3. Repeat the survey routes more than once, because owl call activity is not constant between nights.
4. Information on the environmental conditions should be recorded at each stop. This information can be tested, to determine how environmental conditions affect call rates.
5. Broadcast surveys can be used to survey certain species of owls, but other methods need to be used to survey other species that do not respond well to broadcasts.

ACKNOWLEDGMENTS

We would like to acknowledge and thank the volunteers and research assistants that helped with the broadcast surveys: Stephen Glendinning, Matt Smith, Ben Olsen, André Legris, Warren Schaffer, Rich Russell, Jim Beck, Jennifer Gammon, Brent Flesher, Adele Lareme, and Mark Piorecky. We thank Jim Beck, Gordon Court, Dan Farr, Jason Duxbury, and Barb Beck for their research input. This study was supported by: Foothills Model Forest, Environment Canada (Canadian Wildlife Service and Environmental Assessment Research Fund, Prairie and Northern Region), Alberta Sport, Recreation, Parks and Wildlife Foundation, Edmonton Natural History Club (STEP and SCPP), Canadian Circumpolar Institute, Department of Renewable Resources at the University of Alberta, and Mountain Equipment Co-op.

LITERATURE CITED

Anderson, D.R., Laake, J.L.; Crain, B.R.; Burnham, K.P. 1979. Guidelines for line transect sampling of biological populations. Journal of Wildlife Management. 43(1): 70-78.

Beck, B.; Beck, J. 1988. The greater Edmonton owl prowl. Alberta Naturalist. 18(3): 97-100.

Bosakowski, T. 1987. Census of Barred Owls and Spotted Owls. In: Nero, R.W.; Clark, R.J.; Knapton, R.J.; Hamre, R.H., eds. Biology and conservation of northern forest owls: symposium proceedings; 1987 February 3-7; Winnipeg, MB. Gen. Tech. Rep. RM-142. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 307-308.

Devereux, J.G.; Mosher, J.A. 1984. Breeding ecology of Barred Owls in the central Appalachians. Raptor Research. 18(2): 49-58.

Craighead, J.J.; Craighead, F.C., Jr. 1969. Hawks, owls, and widlife. New York, NY: Dover Publications, Inc. 443 p.

Eberhardt, L.L.; Thomas, J.M. 1991. Designing environmental field studies. Ecological Monographs. 61(1): 53-73.

Fuller, M.R.; Mosher, J.A. 1981. Methods of detecting and counting raptors: a review. In: Ralph, C.J.; Scott, J.M., eds. Estimating numbers of terrestrial birds. Studies in Avian Biology. 6: 235-246.

Fuller, M.R.; Mosher, J.A. 1987. Raptor survey techniques. In: Giron Pendleton, B.A.; Millsap, B.A.; Cline, K.W.; Bird, D.M., eds. Raptor management techniques manual. Washington, DC: National Wildlife Federation: 37-65.

Gill, F.B. 1990. Ornithology. W.H. Freeman and Company. 660 p.

Giron Pendleton, B.A.; Millsap, B.A.; Cline, K.W.; Bird, D.M. 1987. Raptor management techniques manual. Washington, DC: National Wildlife Federation. 420 p.

Johnson, B.T.; Haight, L.T.; Simpson, J.M. 1981. Playback recordings as a special avian censusing technique. In: Ralph, C.J.; Scott, J.M., eds. Estimating number of terrestrial birds. Studies in Avian Biology. 6: 68-75.

McGarigal, K.; Fraser, J.D. 1985. Barred Owl responses to recorded vocalizations. Condor. 87(4): 552-553.

Mosher, J.A.; Fuller, M.R. 1996. Surveying woodland hawks with broadcasts of Great Horned Owl vocalizations. Wildlife Society Bulletin. 24(3): 531-536.

Newton, I. 1979. Population ecology of raptors. Vermillion, SD: Buteo Books: 13-17.

Nicholls, T.H.: Fuller, M.R. 1987. Territorial aspects of Barred Owl home range and behavior in Minnesota. In: Nero, R.W.; Clark, R.J.; Knapton, R.J.; Hamre, R.H., eds. Biology and conservation of northern forest owls: symposium proceedings; 1987 February 3-7; Winnipeg, MB. Gen. Tech. Rep. RM-142. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 121-128.

Pendleton, B.A.; Giron, B.A.; Millsap, B.A.; Cline, K.W.; Bird, D.M. 1987. Raptor management techniques manual. Washington, DC: National Wildlife Federation. 420 p.

Smith D.G. 1987. Owl census techniques. In: In: Giron Pendleton, B.A.; Millsap, B.A.; Cline, K.W.; Bird, D.M., eds. Raptor management techniques manual. Washington, DC: National Wildlife Federation: 304-309.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management. 47(4): 893-901.

APPENDIX A:

Sample data sheet used in the field for owl broadcast surveys in the Foothills Model Forest, Alberta, Canada.

Owling Transects Data Sheets

Date:_______________ Observer(s):_____________________ Transect:______________________

____

Owls Species
BAOW-barred
BOOW-boreal
NSWO-saw-whet
NPOW-pygmy
GHOW-great-horned
GGOW-great gray
NHOW-hawk-owl
LEOW-long-eared

Interval
0 first 2 minutes
1 after first broadcast
2 after second broadcast
3 after third broadcast
4 after fourth broadcast
5 after fifth broadcast
6 after sixth broadcast
7 five minute interval after
8 ten minute interval beyond

Response Type
1 sings, does not approach
2 sings, approaches
3 silently approaches, sings
4 silently approaches, no vocalization

Tree Species
Aw aspen
Pb balsam poplar
Bw paper birch
Sw white spruce
Sb black spruce
Pl lodgepole pine
Lt tamarack
Fa subalpine fir

Point: 1 Start Time:________ Temp.:________°C Wind:________ Prec.:________
Cloud cover:_______% Moon phase:_________ Snow depth: ________

Time	Interval	Owl Species	Direction	Distance	Response	Comments

Point: 2 Start Time:________ Temp.:________°C Wind:________ Prec.:________
Cloud cover:_______% Moon phase:_________ Snow depth: ________

Time	Interval	Owl Species	Direction	Distance	Response	Comments

An Update of Demographic Estimates for Northern Spotted Owls (*Strix occidentalis caurina*) from Oregon's Central Coast Ranges

James A. Thrailkill[1], Robert G. Anthony[1], and E. Charles Meslow[2]

Abstract.—Demographic characteristics of the Northern Spotted Owl (*Strix occidentalis caurina*) were studied on the Eugene District Bureau of Land Management, central Oregon Coast Ranges from 1989-1995. Survival rates were estimated from capture histories of banded owls using Cormack-Jolly-Seber open population models. We banded 233 owls, including 119 that were ≥ 3 years old, 15 that were 1 or 2 years old, and 99 juveniles. Among year variation in the proportion of pairs nesting and fecundity of females was significant ($P < 0.001$). Estimates of apparent annual survival from the selected capture-recapture models were 0.306 (SE = 0.064) for juveniles and 0.875 (SE = 0.018) for subadult and adult owls combined. The estimated annual rate of population change (0.939, SE = 0.045) was < 1.00 ($P = 0.005$) over the 6 years of study, suggesting an average population decline of 6.1 percent per year. Counts of territorial owls decreased by 37 percent from 1990-1995 on the Wolf Creek density study area, a smaller area within the larger surrounding study area. We suggest the owl population decline was due to the reduction of spotted owl habitat.

In 1990 we initiated a demographic study of Northern Spotted Owls (*Strix occidentalis caurina*) on the western half of the Eugene District of the Bureau of Land Management (BLM) which is located in the central portion of the Oregon Coast Ranges. Anderson *et al.* (1990) identified the central Coast Ranges of Oregon as an "Area of Special Concern" because this region has been heavily impacted by timber harvest reducing both the quantity and quality of owl habitat. Thomas *et al.* (1990) argued for the use of demographic parameter estimates to infer the rate and direction of population change for spotted owls. The primary purpose of the study was to provide information on demographic performance and population trends of Northern Spotted Owls in a highly modified forest environment. We also believed that this project would provide information on the effects of forest management practices on the species (Thomas *et al.* 1993a).

At the request of the United State Secretaries of Agriculture and Interior, a workshop was convened in Fort Collins, Colorado in December 1993 to examine all existing demogrpahic data on the Northern Spotted Owl. A main objective of the workshop was to review the demographic information from 11 study areas located throughout the range of the owl before implementation of Option 9 of the President's Northwest Forest Plan (Thomas *et al.* 1993b). The results were subsequently provided to the U.S. Forest Service (USFS) and BLM for inclusion in their planning documents. In addition, results from the individual study areas and a meta-analysis of the entire data set form the basis of chapters that comprise the publication Studies in Avian Biology No. 17.

Following the Fort Collins workshop, most of the spotted owl demography studies continued, as per one of the recommendations of the workshop. Specifically, the Eugene District BLM study continued for 2 additional years and was completed in 1995. The purpose of this paper is to provide an update of the Eugene BLM owl demographic estimates incorporating the 2 additional years of data and also to include results of analyses conducted on parameters (i.e., movements and turnover) not incorporated in our earlier work. Specific objectives of the study were to estimate age-specific survival, birth, and reproductive rates of territorial spotted owls. We also provide information on trend in numbers of territorial owls detected within a smaller portion of the area, the Wolf Creek Density Study Area.

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[2] Northwest Field Representative, Wildlife Management Institute, 8035 NW Oxbow Drive, Corvallis, OR 97330.

STUDY AREA

The 1,432 km^2 study area is located in the central Coast Ranges, 30 km west of Eugene, Oregon (fig. 1). Contained within the larger general study area is the Wolf Creek Density Study Area (DSA) (425 km^2). Throughout the study area, intermingled land ownership produces a checkerboard pattern of alternating square mile sections (1.6 km^2) that are administered by BLM (43.0 percent), State of Oregon (5.0 percent), private industrial timber companies and "other" ownerships (52.0 percent) (fig. 1). Historically, the majority of both federal and privately owned lands were managed for timber production, with clearcutting of late-successional forest (>80 years old) being the major harvest method (Thrailkill *et al.* 1997). Topography is characterized by steep mountain slopes with narrow ridges and elevations ranging from 120 to 870 m. Climate is moderate maritime with most precipitation falling as rain during October-May. The study area is bounded on the north, west, and south by four other spotted owl demographic study areas (Franklin *et al.* 1996), which facilitated the reobservation of dispersing owls. East of the study area is the south terminus of the Willamette Valley, a non-forested agricultural and urban/suburban valley.

Located within the western hemlock (*Tsuga heterophylla*) vegetation zone, the study area is dominated by forests of Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (Franklin and Dyrness 1973). Through field inspections and interpretation of 1990 aerial photography, polygons were delineated that represented suitable, dispersal, and nonsuitable spotted owl habitat, 22, 28, and 50 percent respectively (Thrailkill *et al.* 1996). Old forest, in which the dominant overstory trees are >200 years old, comprises 11 percent of the suitable habitat on the study area (fig. 2). Thomas *et al.* (1990) considered old forest as "superior" owl habitat. Suitable habitat within the DSA (24 percent) was similar to the surrounding general study area (21 percent). Please refer to Thrailkill *et al.* (1996) for a complete description of the habitat cover-types and study area.

METHODS

Field Data Collection

Personnel on the Eugene BLM District began a spotted owl monitoring and banding program in 1986. Although our study did not formally begin until 1990, we included the cohort of owls banded by district personnel in 1989 (28 percent of our total sample) in our estimates of survival and fecundity. In 1990 we began systematic annual surveys (March-August) across the checkerboard ownership pattern of BLM, State of Oregon, and privately owned industrial forest lands to capture and mark unbanded owls and re-observe previously banded owls. Field methods used for surveying, locating, determining sex, capturing, reobserving, and banding spotted owls followed Forsman (1983), Miller *et al.* (1990), Franklin *et al.* (1996), and Thrailkill *et al.* (1996). Four spotted owl age-classes were distinguished: juveniles (J), subadults (1-year-old [S1] and 2-year-old [S2] owls) and adults (≥ 3-yr-old) (Forsman 1981, Moen *et al.* 1991).

Survey effort on the Wolf Creek Density Study Area was consistent from 1990-1995 and consisted of complete coverage of the area with six replicate nighttime surveys each year during the nesting season (March-August). Within this area we attempted to confirm and band any owls that were encountered and determine their reproductive status (i.e., nesting status and number of young fledged).

Within the general study area (DSA excluded), we surveyed all known (historic) owl territories each year, to confirm presence of banded owls, band unbanded owls, and determine their reproductive status. Surveys of the territories were consistent each year and included six replicate nighttime surveys before concluding a territory (territory analogous to an owl site) was unoccupied in a given year. We defined an owl territory as a 2.4 km (1.5 mi) radius centered on an owl nest tree (or principal day roost site). This distance corresponded to the median annual home range size of an owl pair within this province as computed by the minimum convex polygon algorithm (Thomas *et al.* 1990:193-200). Surveys were also conducted in suitable owl habitat located between territories with the number of replicate surveys differing by year (1990:0-3 nighttime surveys, 1991-1995:5-6 nighttime surveys).

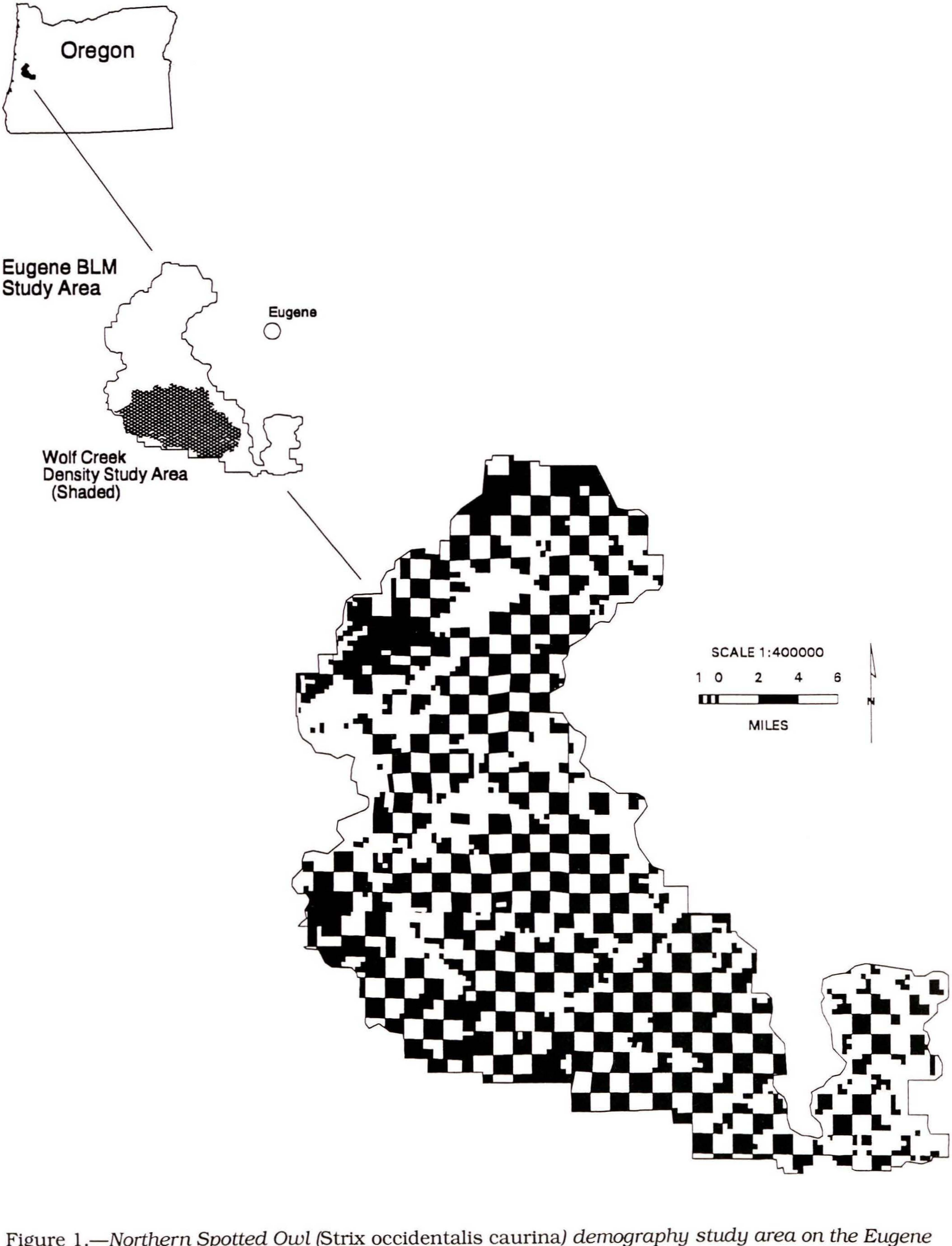
Oregon
Eugene BLM
Study Area
Eugene
Wolf Creek
Density Study Area
(Shaded)
SCALE 1:400000
1 0 2 4 6
MILES
N

Figure 1.—*Northern Spotted Owl (*Strix occidentalis caurina*) demography study area on the Eugene District Bureau of Land Management, central Oregon Coast Ranges, 1990-1995. Shaded sub-plot indicates location of the Wolf Creek density study area (DSA) within the larger surrounding general study area. BLM ownership is represented by black sections interspersed with white sections of non-federal ownership.*

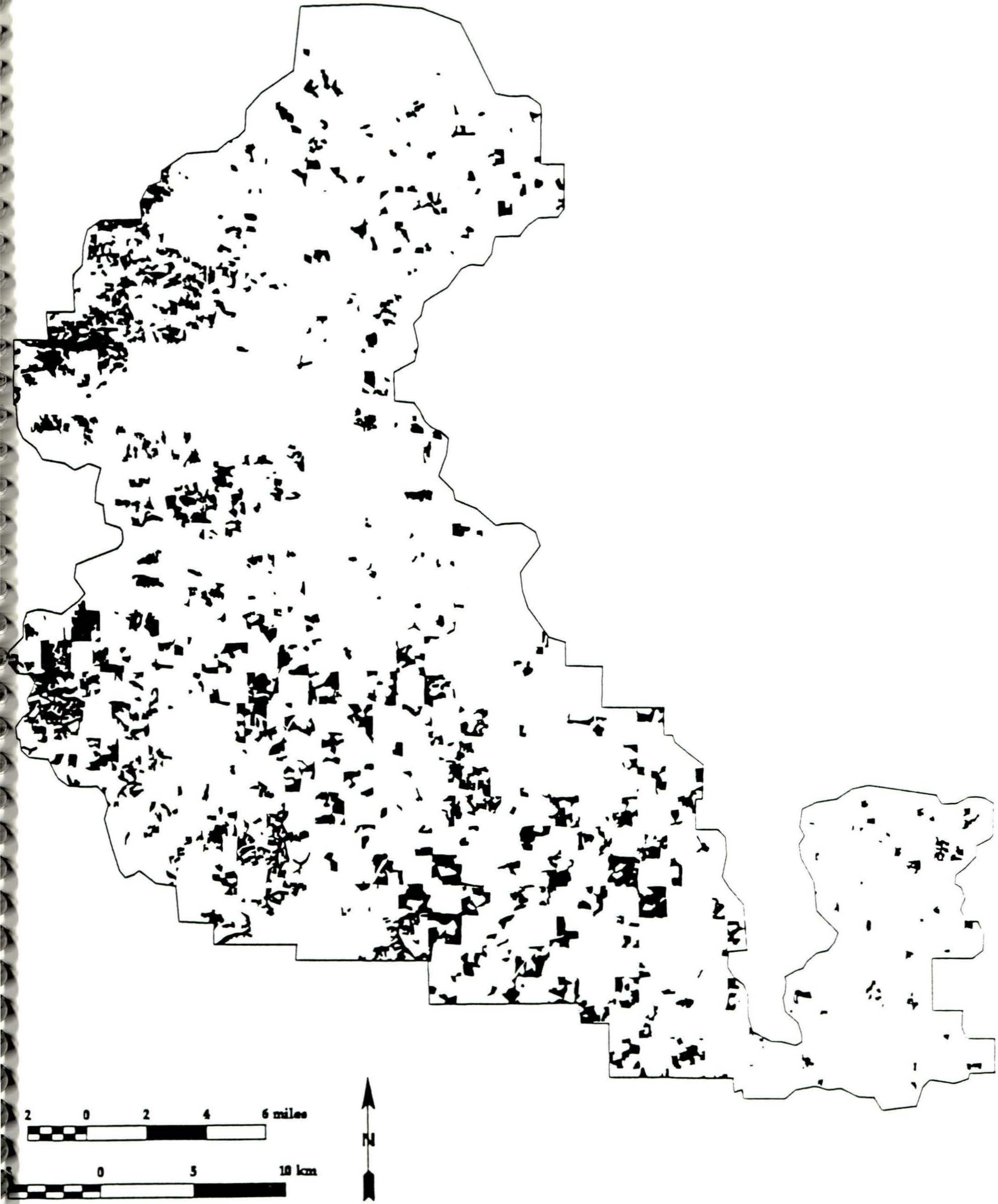

Figure 2.—*Old and mature forest (> 80 years old) habitat patches on the Eugene District BLM Northern Spotted Owl (*Strix occidentalis caurina*) demography study area, central Oregon Coast Ranges, 1990.*

Data Analysis

We used simple linear regression to assess annual trends in the number of owls detected in the Wolf Creek Density Study Area. Turnover rates were calculated as the proportion of marked territorial adult and subadult owls replaced by another individual or found missing from their territories for at least 1 year (Thrailkill *et al.* 1997). Annual turnover rates were a function of adult and subadult mortality, movements of banded birds between territories, and reoccupation and abandonment of territories.

Annual variation in proportions of pairs nesting and pairs checked for reproductive activity were analyzed using chi-square tests. Confidence intervals (95 percent) around mean proportions were calculated following Zar (1984:378-379). Mean fecundity (b_x) was estimated for each age-class as the average number of female young produced per female each year. We assumed a 1:1 sex ratio and included all young located during the breeding period in fecundity estimates (Franklin *et al.* 1996). Annual variation in fecundity was analyzed using an ANOVA (Zar 1984:162-170).

Distance of owl inter-territorial movements and emigration (owls that moved off the study area and were re-observed) by age-class was examined. A movement was defined as a territorial owl relocating for at least 1 breeding season ≥ 2.4 km from their previous nest/activity area. A minimum emigration rate for the adult/subadult cohort was computed by dividing the number of emigrated owls by the total number of banded territorial owls.

Goodness-of-fit tests 2 and 3 in program RELEASE were used to determine if the capture-recapture data met the assumptions of the Cormack-Jolly-Seber capture-recapture model (Burnham *et al.* 1987, Franklin *et al.* 1996, Pollock *et al.* 1985). Survival and recapture rates were estimated using program SURGE (Lebreton *et al.* 1992). Notation of capture-recapture models included subscripts that indicated if a particular model included sex effects (s), age effects (a), non-linear time effects (t), or linear time trends (T). Akaike's Information Criterion (AIC) (Akaike 1973) was used to identify the most parsimonious model (Burnham and Anderson 1992, Franklin *et al.* 1996, Lebreton *et al.* 1992).

The estimated mean annual rate of population change (lambda) during the period of study was computed from age-class estimates of annual survival (juvenile and non-juvenile) and the mean estimate of fecundity for all females ≥ 1 year old (Franklin *et al.* 1996). Estimates of the rate of population change refer to the resident territorial population, which contained several age classes.

RESULTS

Territory Occupancy and Turnover Rates

A sample of 44 territories was known and monitored in 1990. The cumulative number of territories monitored increased by 55 percent through 1995 and approached an asymptotic level in 1994 (fig. 3). The greatest increase in the number of territories occurred between 1991 and 1992 where we recorded a 26.5 percent gain by the end of the season. We attribute this increase in known territories to an increase in the number of field biologists, increase in survey effort, and an enlargement of the study area by 181 km^2 (+ 3 territories); it was not due to an increase in the number of owls on the study area. We attribute the observed increase during the last 2 years to internal emigration (owls abandoning old territories and inhabiting new territories within the study area), not to a population increase.

Among the last 4 years of study (1992-1995), the total number of occupied territories remained relatively stationary (1990:50, 1991:60,

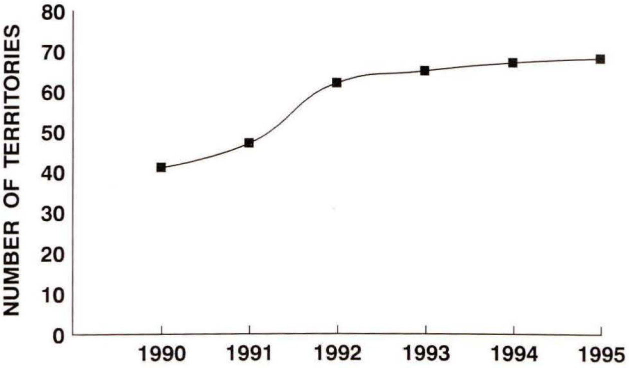

Figure 3.—*Cumulative number of Northern Spotted Owl (*Strix occidentalis caurina*) territories monitored within the Eugene District BLM Northern Spotted Owl demography study area, central Oregon Coast Ranges, 1990-1995.*

1992:56, 1993:54, 1994:53, 1995:53). For both 1994 and 1995 the proportion of unoccupied territories was similar at 0.34 and 0.35, respectively. Annual composition of territories was dominated by pairs (range 1990:0.52-1994:0.78) and secondarily by owls classified as "social status unknown" (fig. 4). The proportion of resident single males was consistently greater than resident single females (fig. 4).

For all years and sexes combined, mean annual turnover rate for individual territorial owls was 25.8 percent. Overall, the frequency of female turnover rates (30.5 percent) was significantly higher than for males (21.2 percent) ($X^2 = 156$, df = 1, P = 0.01). Annually, the percentage of female turnover events was consistently greater than for males (fig. 5).

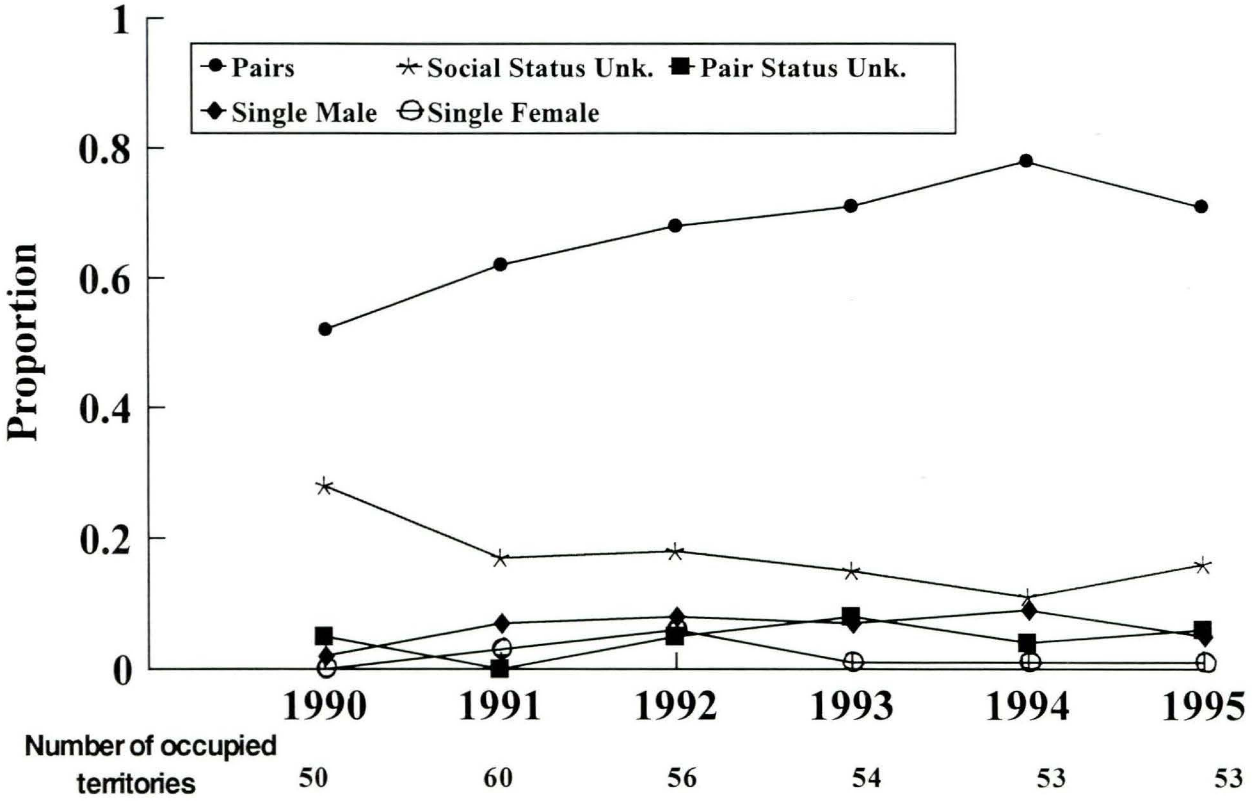

Figure 4.—*Social status of occupied Northern Spotted Owl (*Strix occidentalis caurina*) territories located within the Eugene District BLM Northern Spotted Owl demography study area, central Oregon Coast Ranges, 1990-1995.*

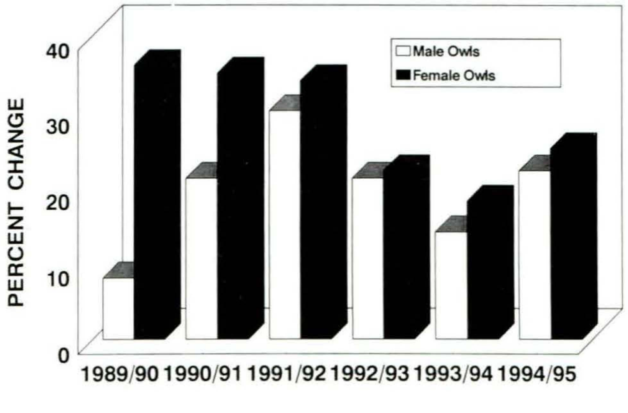

Figure 5.—*Turnover rates of Northern Spotted Owls (*Strix occidentalis caurina*) within the Eugene District BLM Northern Spotted Owl demography study area, central Oregon Coast Ranges, 1989-1995. Overall, the frequency of female turnover rates was significantly higher than for males ($X^2 = 156$, df = 1, P = 0.01).*

Owl Density Within the Wolf Creek Density Study Area

The number of territorial owls detected on the Wolf Creek DSA declined ($r^2 = 0.885$, df 4, P = 0.003) by 37 percent from 1990 through 1995 (fig. 6). Approximately two-thirds (64 percent) of the decline was attributed to owls relocating to territories outside of the DSA. The number of occupied territories also declined significantly ($r^2 = 0.869$, df = 4, P = 0.007) by 36 percent during the study period (fig. 6).

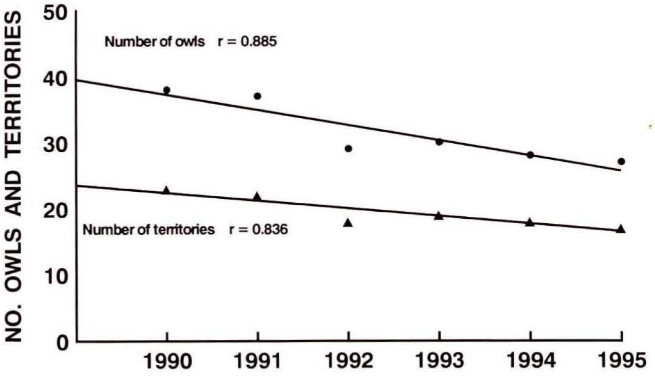

Figure 6.—*Crude density estimates of the number of Northern Spotted Owls (*Strix occidentalis caurina*) and territories within the Wolf Creek DSA (425 km²), Eugene District BLM Northern Spotted Owl demography study area, central Oregon Coast Ranges, 1990-1995. Both the number of territorial owls and occupied territories declined significantly.*

Sex and Age Composition

The male:female sex ratio for all age classes (adults, subadults, and age unknown) was skewed towards males annually. Male owls comprised the greatest proportion of the adult age-class annually, except in 1992. Conversely, for the subadult age-class, females comprised an increasingly greater proportion of this age-class annually except in 1991, whereas, male composition gradually decreased. The number and composition of owls identified as subadults declined during the study (subadult numbers 1990:10, 1991:7, 1992:7, 1993:5, 1994:6, 1995:3). ($r^2 = 0.836$, df = 4, P = 0.011) (fig. 7). The highest ratio of subadults (18.5 percent) to adults (81.5 percent) occurred in 1990, whereas the lowest ratio occurred in 1995 (3.7 percent subadults vs 96.3 percent adults) (fig. 7). Within the age unknown category, the male:female ratio was skewed towards males every year except in 1993 and 1994 when the ratio was 1:1.

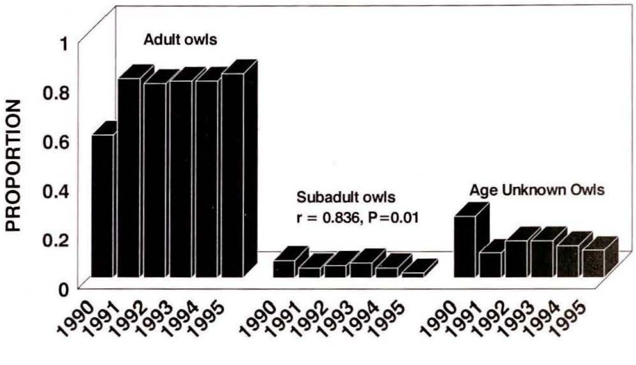

Figure 7.—*Age composition of Northern Spotted Owls (*Strix occidentalis caurina*) detected on the Eugene District BLM Northern Spotted Owl demography study area, central Oregon Coast Ranges, 1990-1995. The number of subadult owls declined significantly during the study.*

Nesting Attempts, Success, and Fecundity

For the 6 years combined, the mean proportion of pairs nesting was 0.44 (n = 177, 95 percent CI = 0.03 - 0.94). However, the proportion of pairs determined to be nesting varied significantly among years ($X^2 = 41.6$, df = 4, P = 0.0001) (fig. 8). The probability of nesting in an

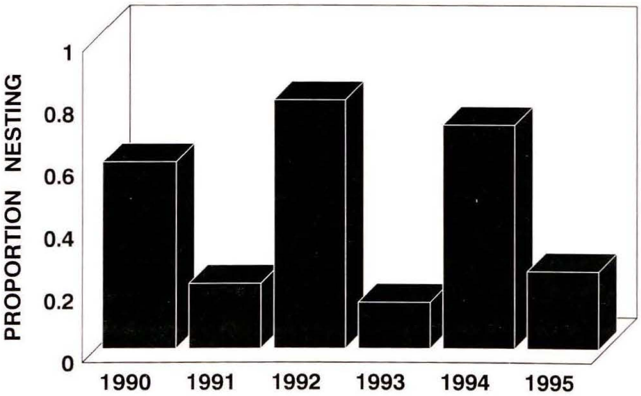

Figure 8.—*Annual proportion of Northern Spotted Owl (*Strix occidentalis caurina*) pairs nesting on the Eugene District BLM Northern Spotted Owl demography study area, central Oregon Coast Ranges, 1990-1995. The proportion of pairs determined to be nesting varied significantly among years ($X^2 = 41.6$, df = 4 P = 0.0001).*

even year was nearly 10 times greater (odds ratio = 9.8) than in an odd year (odds ratio = 1.0) (X^2 = 48.9, df = 1, P = 0.001). The mean proportion of nesting pairs fledging young for the six years combined was 0.64. Conversely, a mean proportion nest failure rate for the 6 years combined was 0.36. This included a low failure rate of 0.04 in 1992 and a high of 0.60 in 1993.

Fecundity, defined as the average number of female young produced per female (assume a 1:1 sex ratio), averaged 0.240 (SE = 0.030) for adult females, 0.068 (SE = 0.050) for subadult females, and 0.223 (SE = 0.028) for all females combined. Successful reproduction by subadult females occurred only two times during this study and each time by a 2-year-old (S2) owl. Fecundity of all females combined varied significantly among years (F = 28.29, 4 df, P < 0.001), ranging from a high of 0.512 in 1992 to a low of 0.039 in 1993 (fig. 9), but no trend with time was evident.

Inter-territorial Movements/Emigration and Dispersal

From 1990-1995, we documented 31 adult/subadult movements ≥ 2.4 km. On average, subadults moved significantly farther than the adults (sexes combined) (t = 4.190, df = 7, P = 0.004) (fig. 10). Within each of the 3 age cohorts, there were no significant differences in the mean distances moved between the sexes (P > 0.05). We recorded a total of 20 dispersals for the juvenile cohort, with the mean dispersal distance being significantly greater than that for adults and subadults (t = 3.797, df = 19, P = 0.001) (fig. 10). The range of dispersal distances (4.8-66.0 km) for all age cohorts of owls was most varied in the juvenile cohort in comparison to either the adults or subadults.

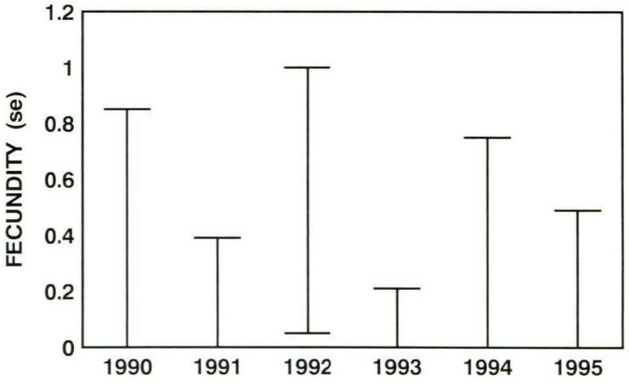

Figure 9.—*Mean annual fecundity of female Northern Spotted Owls on the Eugene District BLM Northern Spotted Owl (*Strix occidentalis caurina*) demography study area, central Oregon Coast Ranges, 1990-1995. Fecundity is defined as the number of female young produced per female owl and assuming a 1:1 sex ratio of young. Fecundity of all females combined varied significantly among years (F = 28.29, df = 4, P < 0.001).*

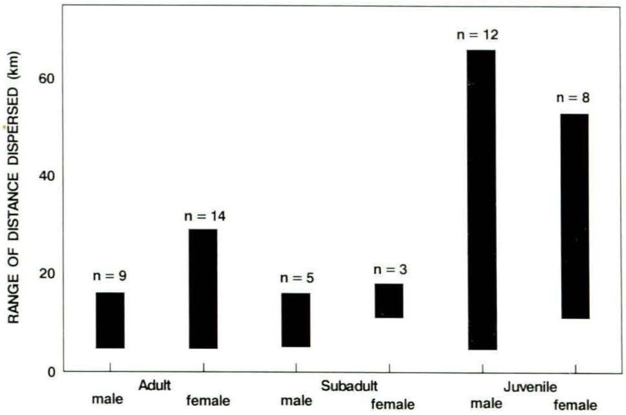

Figure 10.—*Range of distances dispersed by sex and age class for Northern Spotted Owls (*Strix occidentalis caurina*) originally banded within the Eugene District BLM Northern Spotted Owl demography study area, central Oregon Coast Ranges, 1990-1995. On average, subadults moved significantly farther than the adults (sexes combined) (t = 4.190, df = 7, P = 0.004); mean distances moved between the sexes was not significantly different (P > 0.05); juveniles dispersed significantly farther than adults and subadults (t = 3.79, df = 19, P 0.001).*

Of the adults and subadults that dispersed, 67.7 percent were reobserved within the Eugene study area, whereas 32.2 percent were reobserved by biologists on adjacent study areas (fig. 11). We recorded a greater percentage of dispersing females (55 percent) compared to males (45 percent). From 1989-1994 approximately 23.1 percent of the 124 territorial adults and subadults moved to other territories (includes movements both within and outside the study area). Of this total, 6.5 percent relocated to adjacent study areas. Of

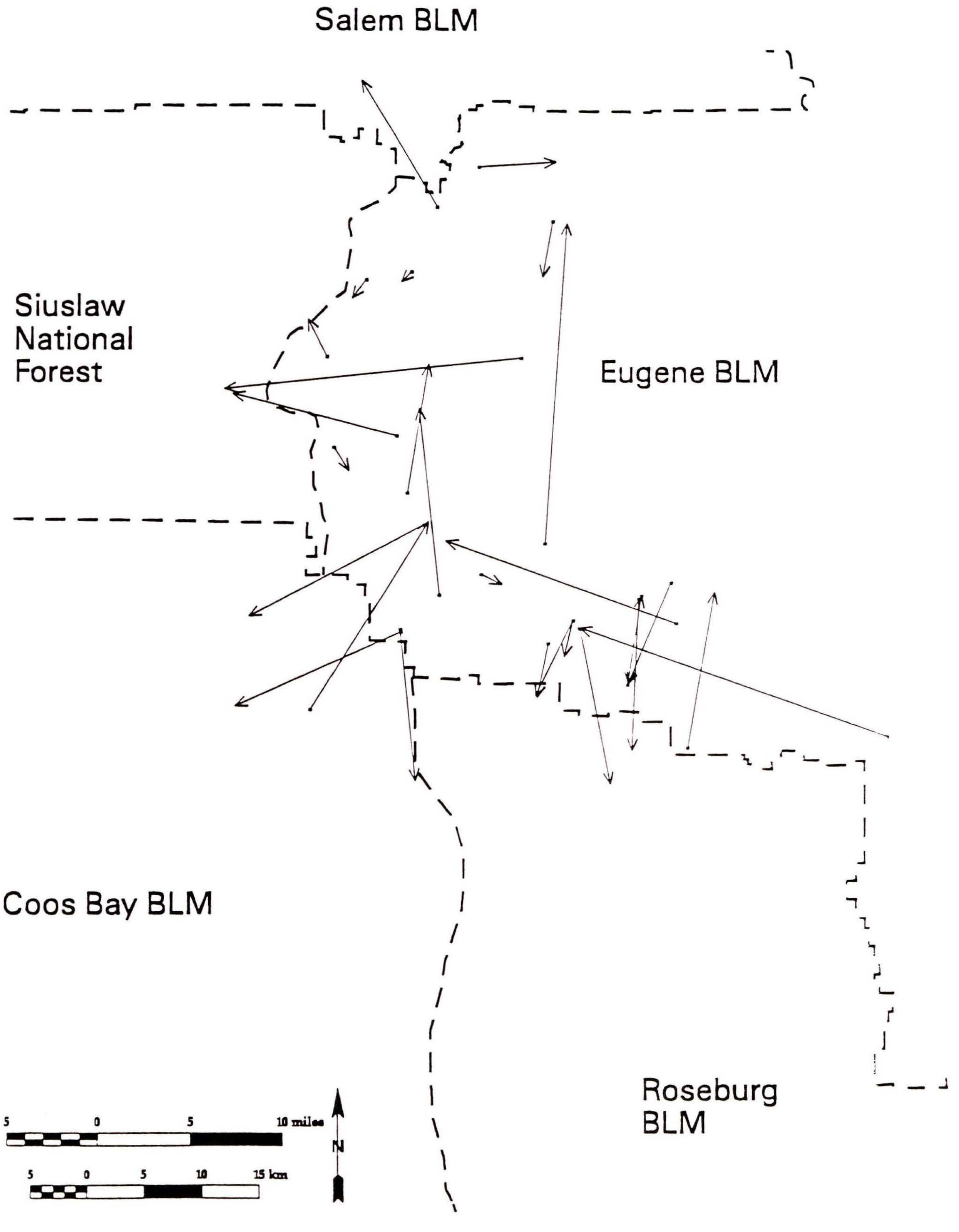
Salem BLM
Siuslaw National Forest
Eugene BLM
Coos Bay BLM
Roseburg BLM
5
0
5
10 miles
5
0
5
10
15 km
N

Figure 11.—*Adult and subadult Northern Spotted Owl (*Strix occidentalis caurina*) movements recorded through color-band reobservations, Eugene BLM District Northern Spotted Owl demography study area, central Oregon Coast Ranges, 1990-1995.*

juvenile owls originally banded within our Eugene study area and encountered 1 or more years later, 30 percent were reobserved within our study area whereas 70 percent were reobserved on adjacent areas (fig. 12).

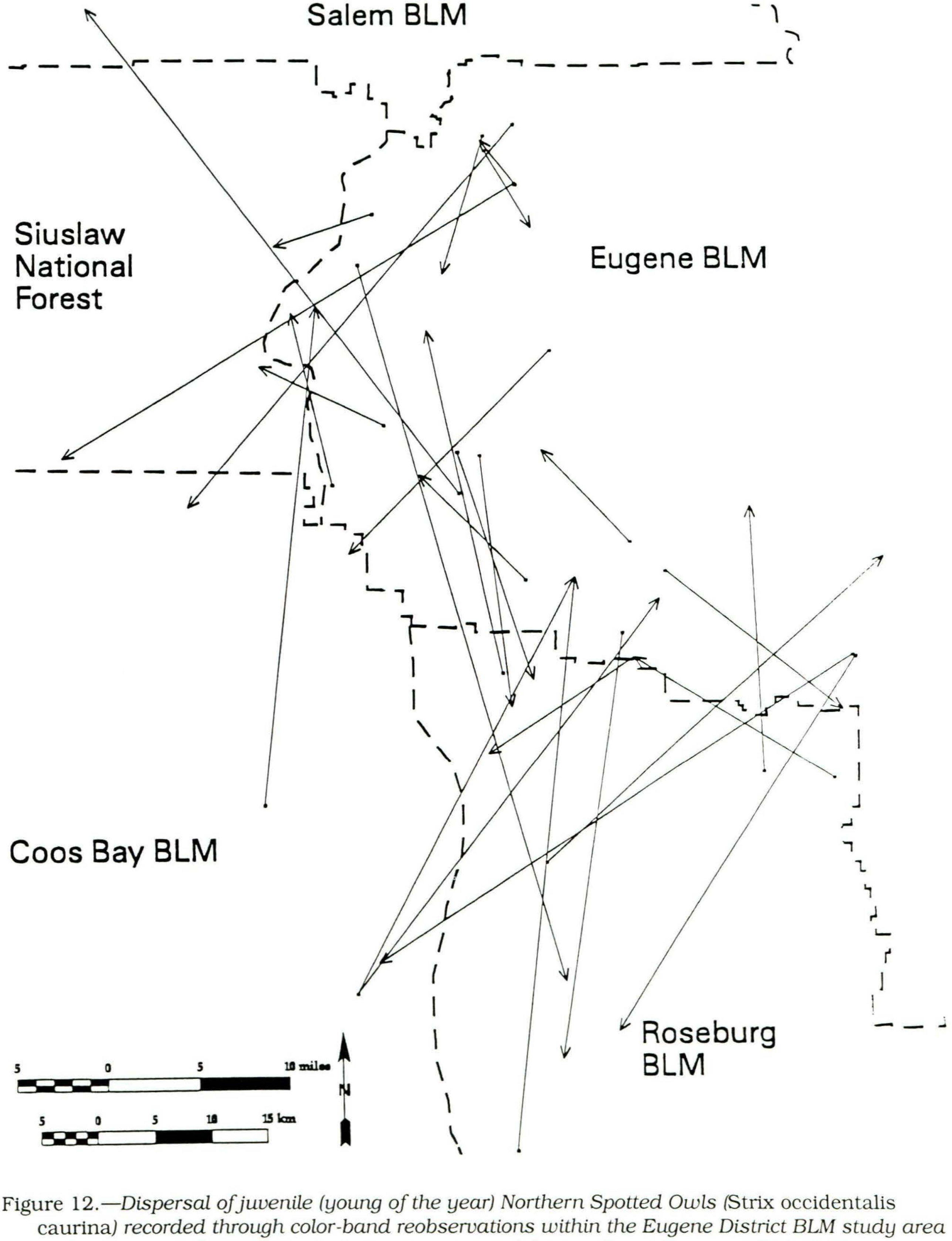
Salem BLM
Siuslaw National Forest
Eugene BLM
Coos Bay BLM
Roseburg BLM
5 0 5 10 miles
5 0 5 10 15 km
N

Figure 12.—*Dispersal of juvenile (young of the year) Northern Spotted Owls (*Strix occidentalis caurina*) recorded through color-band reobservations within the Eugene District BLM study area and immigrants from adjacent study areas, central Oregon Coast Ranges, 1986-1995.*

Capture-Recapture Population

We banded 233 owls from 1989-1995, including 119 adults, 15 subadults, and 99 juveniles (table 1). The sample also included 10 owls (7 females and 3 males) that were banded on adjacent study areas and subsequently immigrated to our study area. The straight-line distance moved by immigrant adults ranged from 3.2-43 km.

Goodness-of-Fit and Model Selection

Goodness-of-fit tests 2 and 3 in the program RELEASE indicated good fit of the capture history data for adult owls (males $X^2 = 9.32$, 13 df, $P = 0.744$; females $X^2 = 8.99$, 10 df, $P = 0.532$); therefore the Cormack-Jolly-Seber open population models were appropriate for the data. The results for Test 3 indicated that owls had similar future expected fates. Results from Test 2 indicated that data for the various age and sex classes were statistically independent. We had so few recaptures of owls banded as juveniles or as subadults that we could not conduct meaningful goodness-of-fit tests for those age groups.

Because of our previous results (Thrailkill *et al.* 1996), we chose to construct models with two age classes, rather than just adults. The most parsimonious model that provided the "best fit" for the two age classes (juveniles and non-juveniles [1-, 2-, and ≥ 3-year-old owls]) was a more "basic" model (ϕ_{a2}, p_{a2}) that held survival and recapture probabilities constant and that did not have time or sex effects. A likelihood ratio test indicated that a competing model ($\phi_{a2 \cdot t}$, p_{a2}) with the next lowest AIC value ($X^2 = 0.559$, df = 1, $P = 0.454$) also fit the data (table 2).

Estimated Survival Rates

Mean annual survival estimates for the two age classes (ϕ_{a2}, p_{a2}) were 0.306 (SE = 0.064) for juveniles and 0.875 (SE = 0.018) for non-juveniles (fig. 13). Estimates of annual survival from a variable time model ($\phi_{a2 \cdot t}$, p_{a2}) are presented here for comparison and generally show a decreasing, although not significant, trend in adult survival (1989:0.98, 1990:0.95, 1991:0.77, 1992:0.84, 1993:0.90, 1994:0.89) ($r^2 = 0.14$, df = 4, $P = 0.465$) (fig. 13). Estimates of annual survival from the selected model and several competing models varied ≥ 2.5 percent for non-juveniles indicating that survival estimates were not greatly affected by model selection (table 2). Estimates of juvenile survival were more variable than for non-juveniles, differing as much as 8 percent among models. The estimate of juvenile survival from the best model was near the upper end of the range of survival estimates produced by the best two-age-class models.

Annual Rate of Population Change

The estimated annual rate of population change on the study area was 0.939 (SE = 0.045), which was significantly < 1.0 ($P = 0.005$). This suggested an average decline of territorial owls of 6.1 percent per year over the 6 year study period.

Table 1.—*Number of Northern Spotted Owls (*Strix occidentalis caurina*) banded and used in capture-recapture analyses on the Eugene District BLM study area, central Oregon Coast Ranges, 1989-1995.*

	Adults (> 3 yrs old)		Subadults (1 or 2 yrs old)			
Year	Female	Male	Female	Male	Unknown	Juveniles
1989	16	22	1	1	0	8
1990	4	5	3	4	1	13
1991	20	15	1	1	0	8
1992	8	3	0	0	0	37
1993	4	4	2	0	0	3
1994	2	7	0	0	0	16
1995	5	4	1	0	0	14
Total	59	60	8	6	1	99

Table 2.—*The "best candidate" two-age-class (juvenile and non-juvenile [≥ 1 year old) capture-recapture models for Northern Spotted Owls (*Strix occidentalis caurina*) on the Eugene District BLM study area, central Oregon Coast Ranges, 1989-1995.*

Model[1]	Deviance	K[2]	AIC[3]	ϕ[4]
$\{\phi_{a2,} p_{a2}\}$	546.453	4	554.453	0.875
$\{\phi_{a2*t,} p_{a2}\}$	528.278	14	556.278	0.888
$\{\phi_{a2*s,} p_{a2}\}$	546.332	5	556.332	0.870
$\{\phi_{a2'',} p_{a2}\}$	546.389	5	556.389	0.887
$\{\phi_{a2,} p_{a2+T}\}$	546.450	5	556.450	0.895
$\{\phi_{a2+t,} p_{a2}\}$	538.709	9	556.709	0.878
$\{\phi_{a2,} p_{a2*T}\}$	545.504	6	557.504	0.895
$\{\phi_{a2,} p_{a2*s}\}$	545.594	6	557.594	0.875
$\{\phi a_{2*T,} p_{a2}\}$	545.873	6	557.873	0.871
$\{\phi_{a2*t,} p_{a2'*s}\}$	527.934	15	557.934	0.886

[1] Parameters are subscripted s for sex, t for time (year) with no linear trend, and T for time as a linear trend. An asterisk (*) indicates interactions. Additive effects in models are denoted with a "+".

[2] K is the number of estimatable parameters from the model.

[3] AIC (Akaike's Information Criterion) is used to select objectively an appropriate "best" model (Akaike 1973).

[4] ϕ = estimate of survival for non-juvenile owls; p = probability of resighting individual owls.

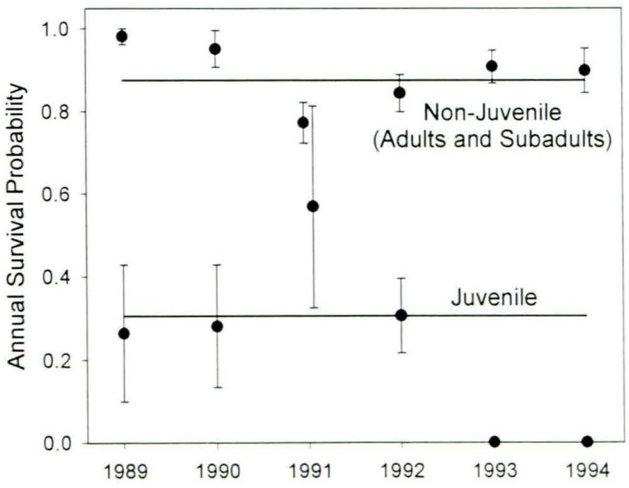

Figure 13.—*Estimates of annual survival probabilities for non-juvenile (> 1 year old) and juvenile Northern Spotted Owls (*Strix occidentalis caurina*) on the Eugene District BLM demography study area, central Oregon Coast Ranges, 1989-1995. Solid line represents a constant trend in annual survival estimates for non-juveniles and juveniles from the most parsimonious age-class model (ϕ_{a2}, p_{a2}). Point estimates and SE's of annual survival from a variable time model ($\phi_{a2*t,}$ p_{a2}) are shown for comparison.*

DISCUSSION

Territory Occupancy and Turnover

The number of occupied territories in the entire study area remained relatively stationary over the last 4 years; however, the population appeared to be constantly undergoing some manner of social change which was reflected by the relatively high turnover rates and proportion of inter-territory movements. This social change occurred within approximately 26 percent of the population while relatively little change occurred among a large proportion of the older owls occupying territories. We believe this social instability is most likely related to low habitat quality within our study area. Only 22 percent of the study area is comprised of suitable owl habitat; of that, only 11 percent is old forest. In contrast, a similar project area in the central Cascades of Oregon is comprised of approximately 55 percent suitable habitat and has relatively lower annual rates of turnover (18 percent, K. Swindle, unpubl. data, 1987-1994). Thomas *et al.* (1990:266) used population models and showed that when a landscape has < 20 percent suitable habitat, the probability that an owl will find a suitable territory is almost insurmountable. Bart and Forsman (1992) found that site occupancy and productivity were lower in areas with < 40 percent suitable habitat. Similarily, we present results showing a significant increase in the frequency of turnover events and lower rates of territory occupancy in landscapes with greater amounts of early seral forest (Thrailkill *et al.* 1997).

Owl Density Within the Wolf Creek Density Study Area

Because the best two age class models did not indicate any time effects on recapture probabilities, we assumed that the number of owls estimated on the DSA each year could be compared without any correction for year-to-year differences in detectability. The 37 percent decline (two-thirds attributed to movements) in the number of owls detected on the DSA is most likely a response to the rapid harvest of owl habitat in the 1980's. Approximately 45 percent of the DSA was comprised of suitable habitat in 1984; 18 percent was clearcut harvested from 1985-1990 prior to court- imposed harvest restrictions on federally managed lands. Approximately 4 percent of the habitat was harvested during the study period 1990-1995, with most of the habitat on private lands harvested prior to 1990. What we measured is probably due, in large part, to "lag-effects" of decreasing habitat on both owl abundance and owl demographic parameters. Van Horne (1983) suggested that species densities may reflect conditions in the recent past or temporary present, rather than long-term habitat quality. The combination of declining survival, density, and annual rate of population change, we believe, indicates a non-stationary, declining owl population in response to the rapid removal in suitable habitat in the 1980's.

Reproductive Parameters: Nesting and Fecundity

The significant annual variation in the proportion of territorial females that nested and produced young on our study area could be due to fluctuations in food supply, weather, habitat alteration, or other factors influencing the reproductive physiology or behavior of spotted owls. For example, annual variation in the breeding by Great Gray Owls (*Strix nebulosa*) and Tawny Owls (*Strix aluco*) fluctuates in response to rodent cycles (Duncan 1992, Southern 1970). Preliminary results from a similar spotted owl study in the Oregon Cascades suggests a positive correlation between the proportion of nest attempts and abundance of deer mice (*Peromyscus maniculatus*) (R.G. Anthony, unpubl. data). For a long-lived species like the spotted owl, the population can probably persist through periods of low fecundity as long as they are followed by periods of high fecundity (Noon and Biles 1990).

Juvenile Survival

Our estimates of juvenile survival for the time period of 1989-1995 are 7 percent higher (30 vs 23 percent) than for the previously reported period of 1989-1993 (Thrailkill *et al.* 1996). A primary factor influencing juvenile recapture rates is the duration of study. Burnham *et al.* (1996) showed that studies conducted between 6-8 years tend to provide higher estimates of juvenile survival than shorter studies because additional years of surveys are available to re-observe owls marked as juveniles. Juvenile survival estimates from adjacent long-term study areas in the Oregon Coast Ranges show survival rates are at least 10 percent higher than ours. For example, Reid *et al.* (1996), on

a study area immediately to the south of ours, showed a juvenile survival estimate of 42 percent (adjusted with radio-tagged juveniles = 54 percent) over a 8-year study period. Hopkins *et al.* (1996) showed a juvenile survival estimate of 40 percent on a study area immediately to the north of ours from 1986-1993. A juvenile survival estimate from the central Cascades study population was 0.28 (Miller *et al.* 1996:1987-1993); this estimate is probably negatively biased due to the lack of adjacent study areas to encounter dispersed juveniles.

Adult Survival

Adult survival increased by 2 percent (87.5 percent) compared to Thrailkill *et al.* (1996) for 1989-1993 (85.3 percent). Our adult survival probability was similar, but slightly higher relative to adjacent study populations in the Oregon Coast Ranges. Results of Reid *et al.* (1996) and Hopkins *et al.* (1996) showed adult survival probabilites of 84.3 and 85.1 percent, respectively. The 2 percent increase we observed is most likely attributed to two factors and does not reflect an actual increase in adult survival. The first factor is our almost "complete survey coverage" of suitable habitat throughout the entire study area, which is in contrast to "site only" monitoring designs utilized in the majority of demographic studies. With our survey design, one is more likely to encounter adult owls that make inter-territorial movements. Second, the juxtaposition of our study area to other study areas enhances the opportunity to record owls that emigrate. A bias in estimates of adult survival may occur with permanent emigration of adults. However, Burnham *et al.* (1996) stated that permanent emigration of territorial adults seems to be relatively rare and is not a significant concern in estimating survival rates of adults. Thomas *et al.* (1990) documented only one occurrence of permanent emigration in > 100 radio-marked adult owl years. Based on our recapture data for 1989-1994, 6.5 percent of the territorial adult/subadult owls relocated to adjacent study areas, indicating that this movement would have gone undetected if adjacent studies were not present. This percentage should be considered as a minimum and we suggest that adult emigration in the Coast Ranges possibly occurs to a greater extent than previously documented and also greater than in other areas. For example, a similar study located in the central Oregon Cascades has a relatively lower overall rate of movement (4 percent). The high proportion of movements we have observed is probably a response to the relatively low amounts of suitable habitat.

When adult owls were recaptured in other study areas, their movements are not considered as permanent emigration in our analysis of survival rates. Therefore, our estimated survival rates are not negatively biased due to these known movements. Future analysis of spotted owl trend estimates should attempt to incorporate the potential bias due to permanent emigration of adults and juveniles (Bart 1995). We believe that methods to estimate this bias could be developed using existing data from demographic study areas sharing common boundaries.

Rate of Population Change

The major finding of this study was the average annual population decline of 6.1 percent. Previously, Thrailkill *et al.* (1996) showed a 8.7 percent population decline for the 1989-1993 time period. For this earlier period, we indicated that we did not disagree with this finding, but questioned the magnitude of the decline given the short-term duration of the study and potential biases in juvenile and adult survival rates (Thrailkill *et al.* 1996). The 2.6 percent difference between the study periods is most likely related to the computed increases in both juvenile and adult survival estimates as stated above. Noon and Biles (1990) found that population growth rates are highly sensitive to adult survival rates, with a few percent change in survival causing a similar magnitude of change in population growth estimates. Although the population growth estimate improved, a disturbing declining trend is still evident. The most plausible explanation for the computed population decline, decreased density, declining survival rates, and high proportion of social instability, is the decline in the acreage of suitable habitat. Most likely, the population has been declining slowly for the past 10-15 years, and our findings not only reflect current conditions, but to some degree, account for lag-effects from previous years. At this time, we do not believe it is possible to tell if our findings are indicative of a population that has dropped below a demographic "threshold" (Lamberson *et al.* 1992).

Because spotted owls are long-lived and vital rates may change, monitoring of demographic information on occupancy, survival and fecundity in relation to changing habitat conditions should continue. A priority for future research should be to establish relationships between owl demographic performance and habitat conditions measured at different scales (Raphael *et al.* 1996). In particular, these relationships need to be examined at the scales corresponding to the size of owl breeding and annual home ranges. Consideration should also be given to conducting surveys for spotted owls in habitat outside of demographic areas and among different land use allocations to provide an independent sample for comparison with the demographic area results. This approach would provide a framework for validation monitoring under the President's Northwest Forest Plan.

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LITERATURE CITED

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. In: Petran, B.N.; Csaaki, F., eds. International symposium on information theory. 2d ed. Budapest, Hungary: Akadeemiai Kiadi: 267-281.

Anderson, D.R.; Bart, J.; Edwards, T.C., Jr.; Kepler, C.B.; Meslow, E.C. 1990. Status review: Northern Spotted Owl (*Strix occidentalis caurina*). Portland, OR: U.S. Fish and Wildlife Service. 95 p.

Bart, J.; Forsman, E.D. 1992. Dependence of Northern Spotted Owls on old-growth forests in the western USA. Biological Conservation. 62: 95-100.

Bart, J. 1995. Evaluation of population trend estimates calculated using capture-recapture and population projection methods. Ecological Applications. 5(3): 662-671.

Burham, K.P.; Anderson, D.R.; White, G.C.; Brownie, C.; Pollock, K.H. 1987. Design and analysis methods for fish survival experiments based on release-recapture. American Fisheries Society Monographs. 5. Bethesda, MD. 437 p.

Burnham, K.P.; Anderson, D.R. 1992. Data-based selection of an appropriate biological model: the key to modern data analysis. In: McCullough, D.R.; Barrett, R.H., eds. Wildlife 2001: populations. London, England: Elsevier Applied Science: 16-30.

Burnham, K.P.; Anderson, D.R.; White, G.C. 1996. Meta-analysis of vital rates of the Northern Spotted Owl. Studies in Avian Biology. 17: 92-101.

Duncan, J.R. 1992. Influence of prey abundance and snow cover on Great Gray Owl breeding dispersal. Winnipeg: Department of Zoology, University of Manitoba. Ph.D dissertation.

Forsman, E.D. 1981. Molt of the Spotted Owl. Auk. 98: 735-742.

Forsman, E.D. 1983. Methods and materials for locating and studying Spotted Owls. Gen. Tech. Rep. PNW-162. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station.

Franklin, A.B.; Anderson, D.R.; Forsman, E.D.; Burnham, K.P.; Wagner, F.F. 1996. Methods for collecting and analyzing demographic data on the Northern Spotted Owl. Studies in Avian Biology. 17: 12-20.

Franklin, J.F.; Dyrness, C.T. 1973. Natural vegetation of Oregon and Washington. Gen. Tech. Rep. PNW-8. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station.

Hopkins, D.S.; Logan, W.D.; Forsman, E.D. 1996. Demography of Northern Spotted Owls on the Salem District of the Bureau of Land Management in northwestern Oregon. Studies in Avian Biology. 17: 31-36.

Lamberson, R.H.; McKelvey, K.; Noon, B.R.; Voss, C. 1992. A dynamic analysis of Northern Spotted Owl viability in a fragmented forest landscape. Conservation Biology. 6: 505-512.

Lebreton, J.D.; Burnham, K.P.; Clobert, J.; Anderson, D.R. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monograph. 62: 67-118.

Miller, G.; Blakesley, J.; Bown, R.; Brown, M.; Forsman, E.; Horn, R.; Lint, J.; Meslow, E.C.; Noon, B.; Reid, J.; Thrailkill, J.; Wagner, F.F.; Zabel, C. 1990. Standards and guidelines for establishment and implementation of demographic and density study areas for Northern Spotted Owls. Corvallis, OR: Cooperative Wildlife Research Unit, Oregon State University. 8 p.

Miller, G.S.; DeStefano, S.; Swindle, K.A.; Meslow, E.C. 1996. Demography of Northern Spotted Owls on the H.J. Andrews study area in the central Cascade Mountains, Oregon. Studies in Avian Biology. 17: 37-46.

Moen, C.A.; Franklin, A.B.; Gutierrez, R.J. 1991. Age determination of subadult Northern Spotted Owls in northwest California. Wildlife Society Bulletin. 19: 489-493.

Noon, B.R.; Biles, C.M. 1990. Mathematical demography of spotted owls in the Pacific Northwest. Journal of Wildlife Management. 54: 18-27.

Pollock, K.H.; Hines, J.E.; Nichols, J.D. 1985. Goodness-of-fit tests for open capture-recapture models. Biometrics. 41: 399-410.

Raphael, M.G.; Anthony, R.G.; DeStefano, S.; Forsman, E.D.; Franklin, A.B.; Holthausen, R.; Meslow, E.C.; Noon, B.R. 1996. Use, interpretation, and implications of demographic analyses of Northern Spotted Owl populations. Studies in Avian Biology. 17: 102-112.

Reid, J.A.; Forsman, E.D.; Lint, J.B. 1996. Demography of Northern Spotted Owls on the Roseburg District of the Bureau of Land Management, Oregon. Studies in Avian Biology. 17: 59-68.

Southern, H.N. 1970. The natural control of a population of Tawny Owls (*Strix aluco*). Journal of Zoology, London. 162: 197- 285.

Thomas, J.W.; Forsman, E.D.; Lint, J.B.; Meslow, E.C.; Noon, B.R.; Verner, J. 1990. A conservation strategy for the Northern Spotted Owl. U.S. Government Printing Office 1990-791/20026.

Thomas, J.W.; Raphael, M.G.; Anthony, R.G.; Forsman, E.D.; Gunderson, A.G.; Holthausen, R.S.; Marcot, B.F.; Reeves, G.H.; Sedell, J.R.; Solis, D.M. 1993a. Viability assessments and management considerations for species associated with late-successional and old-growth forests of the Pacific Northwest. The report of the Scientific Analysis Team. Portland, OR: U.S. Department of Agriculture, Forest Service.

Thomas, J.W.; *et al.* 1993b. Forest ecosystem management: an ecological, economic, and social assessment. Portland, OR: Report of the Forest Ecosystem Management Assessment Team. U.S. Department of Agriculture, Forest Service and U.S. Department of Interior, Bureau of Land Management.

Thrailkill, J.A.; Meslow, E.C.; Perkins, J.P.; Andrews, L.S. 1996. Demography of Northern Spotted Owls, Eugene BLM District, Oregon. Studies in Avian Biology. 17: 53-58.

Thrailkill, J.A.; Anthony, R.G.; Meslow, E.C.; Perkins, J.P.; Andrews, L.S. 1997. Demography and habitat associations of the Northern Spotted Owl on the Eugene District Bureau of Land Management, central Oregon Coast Ranges. Draft Final Report. Corvallis, OR: Oregon Cooperative Wildlife Research Unit, Department of Fisheries and Wildlife, Oregon State University.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Mangement. 47: 893-901.

Zar, J.H. 1984. Biostatistical analysis, 2d ed. Englewood Cliffs, NJ: Prentice-Hall.

Breeding Population of the Great Gray Owl (*Strix nebulosa*) in Belarus: Summary of Recent Knowledge

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Abstract.—A nearly isolated Great Gray Owl (*Strix nebulosa* Forster) population of 50-100 breeding pairs exists in southwestern and south-central Belarus and northern Ukraine. It exhibits rather high nesting density in particular forest tracts and is separated from populations in northwestern Russia by several hundred kilometers. No reliable data on residency, postbreeding movements and wintering strategies are available. Twig nests are used for nesting almost exclusively; the proportion of other nest sites was ca. 10 percent. Mean clutch size was 3.4, with 1.3 young produced per breeding attempt. The main adverse factor affecting the population seems to be illegal shooting by local hunters.

The Great Gray Owl (*Strix nebulosa* Forster) inhabits boreal lowland and mountain forests throughout the Holarctic (Bull and Duncan 1993, Mikkola 1983). In Europe, the southern border of its breeding range is poorly known outside Fenno-Scandia, and two recent handbooks give quite different distributional limits within the countries of the former Soviet Union (Cramp 1985, Mikkola 1983). Heimo Mikkola (1983, p. 210), trusting information on breeding Great Gray Owls in east-central Poland in 1966-1971 (Jablonski 1976), recognized that the "Great Gray Owl is much more common in Poland and in the European part of USSR." The most recent available published information on the Great Gray Owl in Belarus (Fedyushin and Dolbik 1967, Nikiforov *et al.* 1984) is not complete or detailed. Furthermore, the information is not easily available to international audiences as it is in Russian. Using published information and unpublished data collected from the 1980-1990's by ourselves and several of our colleagues (listed in Acknowledgment) this paper describes the status of the Great Gray Owl in Belarus.

DISTRIBUTION AND ABUNDANCE

Breeding of Great Gray Owls in northeastern Belarus, and probably adjacent parts of recent Lithuania in the early 19th century, was first reported by Tyzenhauz (1843). He lived mainly in Postavy, Wilno [Vilnius] Government at that time (now the Vitebsk Region of Belarus) and reported this species to be not very rare and stressed its connection with raised bogs. He did not indicate exact localities, but wrote about "our lands," "our forests" having in mind areas widely adjacent to his own town. The second published record was by Shnitnikov (1913). He described two cases of breeding in 1902-1903; one nest and one brood, and several owl observations near Porechie in the Yaselda River valley north of Pinsk. Using these data, along with the understanding that the habitat was very common and typical for Minsk Region at that time, he concluded that Great Gray Owls were common and that they breed in all "suitable habitats", i.e., "large old forests". No records of Great Gray Owls were reported by German ornithologists working in Belarus during World War I. Zetlitz and Trutzschler (1917) who worked previously in our study area, the upper Shchara River (including Tuhavichi, see below) strangely reported that Ural Owls (*Strix uralinsis* Pall.) were not rare in the 1910's; yet they are definitely absent now (own observ., 1990-1996). It seems that the simplest reason for this situation is that they misidentified Great Gray Owls as Ural Owls, but we have had no success finding either Ural or Great Gray Owl specimens or other materials in German collections to help solve this anomaly. Two Great Gray Owl nests were found in the Bialowiez Primeval Forest, Polish-Belarusian border in 1929-1930 (Szczerkowski 1930, Tomialojc 1990). The most precise location given for these nests was "east of Bialowiez village", not "Bialowiez Forest" as mentioned in Cramp (1985, p. 563), and it is not clear if these records were in the Polish or Belarusian parts of the forest (Tomialojc 1990). This was the last information on Great Gray Owls breeding in the region until the early 1970's, and the species was considered extremely rare in Belarus in monographs published after World War II (Dolbik and Dorofeev 1978, Fedyushin and Dolbik 1967, Nikiforov *et al.* 1984). Our review of recent information starts with Demianchik and Gaiduk (1981).

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The distribution of Great Gray Owls in Belarus is summarized in figure 1. Short descriptions of the points shown in figure 1 follow.

1. Bialowiez Forest. Since the breeding records of 1929-1930, six breeding season observations including vocalizing males noted from 1953-1996 (Datskevich *et al.* 1985, Tomialojc 1990).
2. Tuhavichi, Lyahavichi District. This area, as well as areas 3 and 5, is situated around Vygonovskoe Lake. Eleven nests on six territories were found in swamped deciduous forests along the Shchara River floodplain in 1992, 1995, and 1996.
3. Two nests and one brood were reported by Demianchik and Gaiduk (1981) "in the vicinities of Vygonovskoe and Bobrovichskoe Lakes" from 1976-1979.

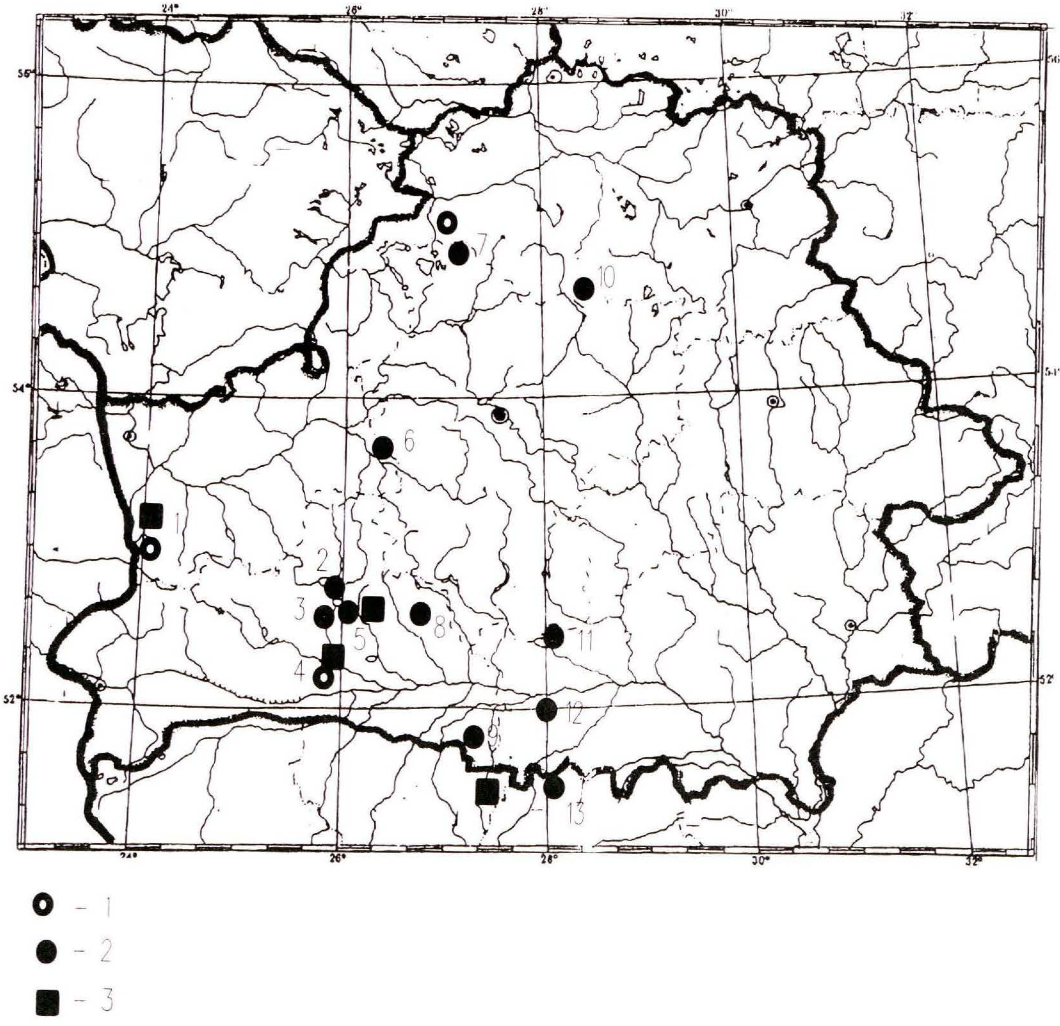

Figure 1.—*Breeding distribution of the Great Gray Owl (*Strix nebulosa*) in Belarus. 1 = old (prior to World War II) breeding localities; 2 = recent (since mid-1970's) breeding localities; 3 = probable breeding localities and breeding season observations.*

4. Porechie, Pinsk District. Shnitnikov's (1913) study area; a single owl was repeatedly observed hunting in the same location in the floodplain in May 1992.
5. Svyatitsa, Lyahavichi District. Six nests on five territories were found in a large wet forest tract interspersed with open mires and bordered by cultivated land from 1994-1996.
6. Kroman Lake, Novogrudok District. A territorial male (1993), a territorial pair (1994), a nest and a territorial male (1995), and no owls (1996) were observed within ca. 10 square km of conifer and mixed forests along Neman River floodplain.
7. NE Myadel District. Two nests ca. 5 km apart were found in the spruce forests in 1976 and 1985, no fieldwork has been carried out in this area since. The area falls within the area mentioned by Tyzenhauz (1843).
8. Deniskovichi, Gantsevichi District. One fledged brood was recorded in 1980 (Dolbik 1985).
9. Olmany, Stolin District. Four nests were found on the edge of and in small forested islands within the huge tract of open transition mires and raised bogs from 1995-1996.
10. Velevshchina, Lepel District. Breeding Great Gray Owls were observed in the same nest in a pine bog along a small river floodplain from 1990-1991; "large" owls bred there in 1993, but the species was not recorded. Owls did not use this nest in 1995 or 1996.
11. Hvoika, Zhitkovichi District. Two nests were found in 1991; prior to this, birds were observed several times during the breeding season. No fieldwork has been carried out in this area since 1991.
12. Pripyatsky Nature Reserve, Zhitkovichi District. Two nests were found in 1980 in habitat similar to that in the Olmany area; fresh feathers were found at two other locations in the Reserve in 1995.
13. Polessky Nature Reserve, Zhitomir Region, Ukraine. Three nests were found from 1985-1988 (Yaremchenko and Sheigas 1991; Zhila 1991), two nests from 1995-1996. A territorial male was observed in neighboring Syra Pogonya Reserve (NE Rivne Region) 1988.

A concentration of breeding records occurs in southwest and south-central Belarus, in the Black Sea-Baltic watershed in the upper Pripyat River basins and tributaries, Narev River, and the upper Neman River. Bialowiez Primeval Forest seems to be the westernmost point of its range in eastern Europe. Despite extensive ornithological research activities only two breeding records were documented in the 1800's in this area. Several confirmed breeding records exist in northern Ukraine; breeding Great Gray Owls are surely absent in the Ukraine outside the northern Polessie Region (Peklo 1994). The southeastern border of its range in Belarus is not clear, but it seems that owls do not breed east of the Pripyat tributaries, Ptich and Ubart.

Considering the known distribution of Great Gray Owls in Europe it seems very surprising that only a few breeding records were noted in northern and central Belarus (only five recent breeding records in two localities in pine, spruce, and conifer-deciduous subtaiga forests of Belarusian Poozerie [northern lake region]). Although there were very few special searches for Great Gray Owls in northern Belarus, its density there seems to be lower than in southwestern and south-central parts of the country. The following arguments support this conclusion.

1. Great Gray Owls in Belarus use primarily old raptor nests for breeding (see below), and most of the nests were found during the checks of known raptor nests. More twig nests suitable for owls were checked in northern and central Belarus than in the south in the late 1980s and 1990s. But the distribution of active Great Gray Owl nests was the reverse. In 1995 and 1996, the most successful years for our nest searches, 206 raptor and Black Stork (*Ciconia nigra* L.) nests were checked in central and northern Belarus while 54 such nests were checked in southern Belarus. No active Great Gray Owl nests were found outside southern Belarus, where we succeeded in finding 19 nests during these 2 years (Chi-square test, $P < 0.01$).
2. Great Gray Owls are extremely rare breeders or are absent in the area to the north, northwest and northeast of the Belarusian border (Leibak *et al.* 1994, LOB 1996, Malchevsky and Pukinsky 1983, Patrikeev 1991, Zalakevicius 1995); only 11 documented breeding records from the 1800's have been reported in the sources mentioned. Furthermore, no Great Gray Owl breeding was observed in Estonia, Latvia,

Lithuania and Poland in 1995-1996, years which seemed to be good for owl breeding in Belarus (A. Avotins, M. Gromadzki, E. Lelov, G. Matiukas, M. Strazds, pers. comm.).

It may be concluded that a rather dense breeding Great Gray Owl population exists in southern Belarus and northern Ukraine. This population seems to be separated from the species' range in northern Europe by vast areas with no or only a few scattered breeding pairs. The history and origin of this population, its connection with northern European populations are completely unknown.

Local densities of Great Gray Owls in Belarus may be very high. In the Tuhavichi study area, few nests were found in 1995 during a survey of a ca. 10 square km forest tract; six nests were found there in 1996. A similar local density was recorded in the Svyatitsa study area in 1995. Four nests in Olmany area were recorded from 1995-1996 while randomly checking 19 raptor and Black Stork nests. Taking into consideration this recent distribution of breeding owls, the area of suitable habitat, and our density data, we estimated the Great Gray Owl breeding population in Belarus to be 50-100 pairs. These figures may be an underestimate and we did not try to estimate the Ukrainian part of the population.

SITE TENACITY AND NEST SITES

There are few data on the territoriality and nest-site tenacity of Great Gray Owls in Belarus. Beginning in the 1995 field season, we monitored the use of known territories in some of our study areas. In total, 70 percent of territories located in 1995 were used in 1996 (N = 10). In Tuhavichi, all four nests were re-used in 1996 (two new nests were also found within 1.5 km of known nests) as well as one nest in Zhitomir Region, but only 40 percent in Svyatitsa from 1995-1996. Other isolated breeding localities (Kroman, Myadel and Velevshchina, see above) exhibited some stability, at least for 2-3 years.

We know almost nothing about the wintering ecology of Great Gray Owls. Winter observations are regularly reported (at least one or two each winter by local hunters) in the northern and northeastern parts of the Vitebsk Region, far from known breeding localities. There is a high probability that these are wandering birds from northern Russia. Very few winter observations on breeding grounds were recorded. Birds (exact number not reported) were shot in December 1956 and February 1960 in Bialowiez Forest (Datskevich *et al.* 1985). We observed owls four times in Svyatitsa and Tuhavichi from 1993-1996 near nest-sites 1.2-1.5 months prior to breeding, as early as February 18.

We hypothesize that Great Gray Owls in Belarus, at least in the south, hold long-term territories and are probably resident. In this respect, they more closely resemble some Swedish and American mountain populations rather than typical Fenno-Scandian ones (Bull and Duncan 1993, Mikkola 1983). Breeding owls in Belarus use a wide variety of forest habitats for breeding, from upland dry coniferous to swampy alder, birch forests, and pine bogs. About two-thirds of known nests were situated in wet deciduous forests, but this distribution seems to be biased due to predominance of this forest type in the most intensively studied Svyatitsa and Tuhavichi areas. Nests were always situated close to open habitats, mainly natural mires, and two were found in several ha. forest islands within large mire tracts.

More than 85 percent of all nests were in large twig nests (table 1), built by raptors, mainly Common Buzzard (*Buteo buteo* L.), Black Storks, and Common Ravens (*Corvus corax* L.). A ground nest was situated near the trunk bases of a group of trees in swampy alder forest. An exact description of beehive nests was not reported (Yaremchenko and Sheigas 1991), but they seem to be similar to stump nests, as local people in Polessie use thick logs

Table 1.—*Nest sites used by Great Gray Owls (*Strix nebulosa*) in Belarus.*

Nest sites	N	Percent (%)
Twig nests of (summary)	25	86
medium-sized raptors	*22*	*75.5*
Black Storks	*2*	*7*
Common Ravens	*1*	*3.5*
Stumps	1	3.5
Hives (bee)	2	7
Ground	1	3.5
Total	29	100

for hive preparation and put these hives in a vertical position on the trees 3-6 m above the ground, often in remote forest areas (unpubl. data). The proportion of stump nests in Belarus (10.5 percent including hive nests) contradicts the hypothesis of Mikkola (1983) on the increased use of this nest-site type toward the southern part of the Great Gray Owl's range, but which was supported by Finnish and American data (Franklin 1988). Some underestimate of less conspicuous stump nests is possible, but it probably does not significantly affect nest-site use (table 1).

BREEDING PERFORMANCE

Clutch initiation dates for Belarusian Great Gray Owls ranged from 30 March to 31 April (table 2). Weather conditions of winter 1995-1996 were steadily cold with thick snow cover which began to thaw only in early April. Snow cover may be important for the onset of breeding in Belarus as in western North America (Franklin 1988). In 1996, three of seven clutches were started mid-April and four in late April. Clutch size (table 3) in Belarus is somewhat smaller than in Fenno-Scandia, reflecting a well-known trend of increased clutches in the northernmost areas (Mikkola 1983). Mean breeding success was 1.34 ± 1.34 fledglings/ active nest (n = 16), six nests failed to produce any fledglings (table 4). Brood reduction was documented for three of 12 nests; in total, five nestlings died. One case of possible bigyny was recorded in Tuhavichi in 1996. Two nests attended by two females were found 250 m apart, one in a raptor nest used successfully in 1995 and another on the ground (no suitable twig nests were available within 500 m). Three young fledged from the first nest, and only one was raised in the other. In the presumably, secondary nest, egg laying occurred ca. 10 days later than in the first, and at least one nestling died.

Unfortunately, the second nest was found only in late May, a period when males were never seen near the nests. Thick leaf cover caused additional difficulties during our observations and so we failed to record the exact number of males near these two nests.

Table 2.—*Breeding phenology of Great Gray Owls (*Strix nebulosa*) in Belarus.*

Period	Clutches started	
	N	Percent (%)
March 20-30	3	14
April 1-9	5	23
April 10-19	8	36
April 20-31	6	27
Total	22	100

Table 3.—*Reproductive output of Great Gray Owls (*Strix nebulosa*) in Belarus.*

Clutch/brood size	Clutches		Broods	
	N	Percent (%)	N	Percent (%)
1	-	-	3	25
2	5	22	4	33
3	7	30	4	33
4	8	35	1	9
5	3	13	-	-
Mean ± SD (N)	3.39 ± 1.05 (23)		2.25 ± 0.97 (12)	

Table 4.—*Reasons of nest failures and mortality of Great Gray Owls (*Strix nebulosa*) in Belarus.*

Failure/mortality reason	Nest failures, N	Birds died, N
Eggs fallen down	1	-
Adults/birds killed by man	2	8 (includes 4 adults and 2 juveniles)
Birds killed by Eagle Owl	-	1 (a juvenile)
Nest abandoned/bird found dead (reasons unknown)	4	3 (includes 1 adult and 1 juvenile)

CONSERVATION ISSUES

The lack of information on the status of Great Gray Owls in the 1960's and 1970's was the reason this species was considered among the most rare and endangered in Belarus (Dolbik and Dorofeev 1978). It currently has the highest national legal conservation status (Dorofeev 1993). Considering potential threats, one can see that its situation is not so bad. There are many forest and mire tracts within the core of the species' range which are not seriously affected by economic activities. Tens of square kilometers of such habitat exists in Ivatsevichi, Lelchitsy, Lyahavichi, Luninets, Stolin and Zhitkavichi Districts. Furthermore, most of the known dense Great Gray Owl populations inhabit nature reserves (Bialowiez Forest, Polessky in Ukraine, Pripyatsky, Telehansky [around Vygonovskoe Lake]) which conserve habitats. Several hundreds of square kilometers of mires and adjacent forests in Olmany have no human population and were used for 30 years as military grounds; plans to create a protected area there are in preparation. Great Gray Owls often share territories with two of their potential predators, the Eagle Owl (*Bubo bubo* L.) and the Goshawk (*Accipiter gentilis* L.) (Mikkola 1983). It seems, however, that predation does not affect their populations seriously. The proportion of Great Gray Owls in the diet of the Eagle Owl (table 4) is less than 0.3 percent (unpubl. data), and this predator is rare in Belarus (Fedyushin and Dolbik 1967, Dorofeev 1993). No owls were recorded as prey of Goshawks in Belarus (Golodushko 1965, Ivanovsky and Umanskaya 1981, unpubl. data).

It seems that illegal shooting by local hunters is the most adverse factor affecting Great Gray Owl populations in Belarus. Mortality counts in table 4 are minimal values known to us from the last 30 years and include killing for scientific collections (four birds). The fearless behavior of Great Gray Owls towards humans may provoke non-educated hunters and makes these birds easy targets. It is impossible to estimate the real importance of this factor, but two positive aspects have to be stressed. First, remote and often swampy forests used by owls for breeding are not regularly visited by humans, at least in spring. During 2 years we did not see people or their tracks closer than 300 m to 15 nests, although some dry trails 300-400 m apart were used rather regularly. Second, the idea of persecution of birds of prey has become less popular in Belarus recently along with an increasing conservation approach.

ACKNOWLEDGMENT

This paper would not be so complete without the kind contribution from our colleagues providing us with some of their unpublished data on Great Gray Owls in Belarus. We wish to cordially thank I. Byshnev, N. Cherkas, V. Dombrovsky, V. Ivanovsky, M. Nikiforov, V. Sidorovich, and V. Yurko for their useful help. Y. Kuzmenko informed us about recent breeding records in the Ukraine. Our thanks are also to A. Avotins, M. Gromadzki, E. Lelov, G. Matiukas, P. Saurola, M. Strazds, and M. Suopajärvi for the information from neighboring countries and fruitful Great Gray Owl discussions.

LITERATURE CITED

Bull, E.L.; Duncan, J.R. 1993. Great Gray Owl (*Strix nebulosa*). In: Poole, A.; Gill, F., eds. The birds of North America. No. 41. Philadelphia, PA: Academy of Natural Sciences; Washington, DC: American Ornithologists' Union: 1-16.

Cramp, S. 1985. Birds of the Western Palearctic. Vol. 4. Oxford, UK: Oxford University Press. 960 p.

Datskevich, V.A.; Popenko, V.M.; Kolosei, L.K. 1985. Composition, numbers and distribution of owls populations in Bialowiez Forest. Zapovedniki Belorussii. Issledovaniya. 9: 106-114 (in Russian).

Demianchik, V.T.; Gaiduk, V.E. 1981. Breeding of Great Gray Owl (*Strix nebulosa* Forst.) in Byelorussian Polessie. Archives of the Academy of Sciences of BSSR. Series of Biological Sciences. 26(5): 115-116 (in Russian).

Dolbik, M.S. 1985. Revision of the composition and distribution of the ornithofauna of Byelorussia. Archives of the Academy of Sciences of BSSR. Series of Biological Sciences. 30(2): 85-89 (in Belarusian).

Dolbik, M.S.; Dorofeev, A.M. 1978. Rare and vanishing birds of Byelorussia. Minsk: Uradzhai. 198 p. (in Russian).

Dorofeev, A.M., chief ed. 1993. Red Data book of the Republic of Belarus. Minsk: Belaruskaya Encyclopedia. 559 p. (in Russian and Belarusian).

Fedyushin, A.V.; Dolbik, M.S. 1967. Birds of Byelorussia. Minsk: Navuka i Technika. 519 p. (in Russian).

Franklin, A.B. 1988. Breeding biology of the Great Gray Owl in southeastern Idaho and northwestern Wyoming. Condor. 90: 689-696.

Golodushko, B.Z. 1965. Raptors and their role in game management of Bialowiez Forest. Minsk: Byelorussian State University. 306 p. Ph.D. dissertation (in Russian).

Ivanovsky, V.V.; Umanskaya, A.S. 1981. Trophic relationships of Goshawk (*Accipiter gentilis* L.) in the northern Byelorussia. Vestnik Zoologii. 14(4): 61-65 (in Russian).

Jablonski, B. 1976. Estimation of bird abundance in large areas. Acta Ornithologica. 16: 23-76.

Latvijas Ornitologijas Biedriba [LOB]. 1996. Latvijas meza putni. Riga: SIA McAbols. 192 p.

Leibak, E.; Lilleleht, V.; Veromann, H. 1994. Birds of Estonia: status, distribution and numbers. Tallinn: Estonian Academy. 287 p.

Malchevsky, A.S.; Pukinsky, Y.B. 1983. Birds of Leningrad Region and adjacent territories: history, biology and conservation. Vol. 1. Leningrad: Leningrad University Press. 480 p. (in Russian).

Mikkola, H. 1983. Owls of Europe. London: T & AD Poyser. 397 p.

Nikiforov, M.E.; Yaminsky, B.V.; Shkliarov, L.P. 1984. Birds of Byelorussia: handbook to nests and eggs. Minsk: Vysheishaya Shkola. 479 p. (in Russian).

Patrikeev, M.V. 1991. Great Gray Owl in Nizhne-Svirsky Nature Reserve. Materials of the 10 All-Union Ornithological conference; 1991 September 17-20; Vitebsk. Part 2, vol. 2. Minsk: Navuka i Technika: 139-140 (in Russian).

Peklo, O.M. 1994. Great Gray Owl. In: Red data book of Ukraine. Wildlife. Kiev: Ukrainska Encyclopedia: 361 p. (in Ukrainian).

Shnitnikov, V.N. 1913. Birds of Minsk Government. Materials to the knowledge of fauna and flora of the Russian Empire. Zoological Division. 12: 1-475 (in Russian).

Szczerkowski, 1930. Dergegenwärtige Zustand der Bialowieser Heidde. Zoologische Garten. 3: 282-285.

Tomialojc, L. 1990. Ptaki Polski, rozmieszczenie i loczebnosc. Warszawa: PWN. 462 p.

Tyzenhauz, K. 1843. Ornitologia powszechna. Vol. I. Wilno.

Yaremchenko, O.A.; Sheigas, I.N. 1991. Great Gray Owl (*Strix nebulosa*) in Polessky nature reserve. Vestnik Zoologii. 24(5): 86 (in Russian).

Zalakevicius, M., comp. 1995. Birds of Lithuania: status, number, distribution (breeding, migration, winter). Acta Ornithologica Lithuanica. 11 (special issue): 1-105.

Zetlitz, O.v.; Trutzschler, O. 1917. Liste der im Gebiete der Schara beobachteten Vödel. Journal f. Ornithologie. 65: 278-308.

Zhila, S.N. 1991. Nesting of Great Gray Owl in the territory of Polessky nature reserve. Vestnik Zoologii. 24 (2): 84-85 (in Russian).

Comparative Food Niche Analysis of *Strix* Owls in Belarus

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Abstract.—Three *Strix* species breed sympatrically in Belarus. The Tawny Owl (*Strix aluco*) is one of two commonest owl species in the country, and is distributed throughout the whole territory. Its' range overlaps widely with two other species, the Ural Owl (*S. uralensis*) which is common in the forests of the northern part and the Great Gray Owl (*S. nebulosa*) which occurs in a rather limited area in the southern region. The diet of all three species was studied from 1986-1996 by the analysis of pellets collected mainly near nests. All owls preyed mainly on voles and shrews, but niche differences between them are apparent. The Great Gray Owl appeared to be a vole specialist, while the Tawny Owl had the most diverse diet, often feeding on mice, anurans, insects, and birds. The food niche of the Ural Owl was between these extremes.

During the last 2 decades, studies on the trophic structure of raptor communities have attracted special attention (Herrera and Hiraldo 1976, Jaksic 1988, Jaksic and Delibes 1987, Jerdzejewski *et al.* 1989). Marti *et al.* (1993) summarized the main results and set research priorities in this area. One of their observations was that a shortage of good quality data on raptor diets limited wide geographic analyses. Hence, I prepared this summary on the diets of these three *Strix* species, Tawny (*S. aluco L.*), Great Gray (*S. nebulosa* Forster), and Ural (*S. uralensis* Pall.) Owls breeding in Belarus. The distribution of these species in Belarus are quite different. The Tawny Owl is widespread, being the second most common owl species in the country (Fedyushin and Dolbik 1967), and widely sympatric, with the other two species inhabiting mainly northern (Ural Owl) and southwestern regions of the country (Great Gray Owl) (Fedyushin and Dolbik 1967, Mikkola 1983). The ranges of the Great Gray and Ural Owls overlap slightly; only few widely dispersed Great Gray Owl pairs are known to breed within the range of the Ural Owl. All three species are small rodent specialists and competitive interactions between them have been reported (Lundberg 1980, Mikkola 1983). My aim was to report on the diet and to provide food niche statistics for all three of these species in Belarus.

MATERIALS AND METHODS

Dietary sampling data were collected in different Districts of Belarus from 1986-1996 (fig. 1). Pellets collected near nests, and to a lesser extent at roosting sites, represent the bulk of the sample. Some additional data were obtained by the extraction of bones from nests after fledging and by stomach analysis (six Tawny Owls and one Ural Owl).

Pellets were carefully dissected with all bone and chitin remnants extracted. Identification and counts of prey species were carried out using the skull and lower jaws for mammals, all bones for birds, pelvic bones for amphibians, and head capsules and elytra for insects. Reference collections and publications (Görner and Hackethal 1988, Puzek 1981) were used to identify prey. Analytical techniques described by Marti *et al.* (1993) were used. Prey weight data were obtained from files of the Belarusian Ornithological Society, unpublished materials of M. Pikulik and V. Sidorovich (Institute of Zoology, Minsk), and my own material. Predator weights were taken from Marti *et al.* (1993).

RESULTS

Data on the prey species studied are given in table 1 and table 2. Shrews and voles appeared to be the most important prey categories for all *Strix* species in Belarus. The Great Gray Owl is a small mammal specialist prefering *Microtus* voles, the other two owl

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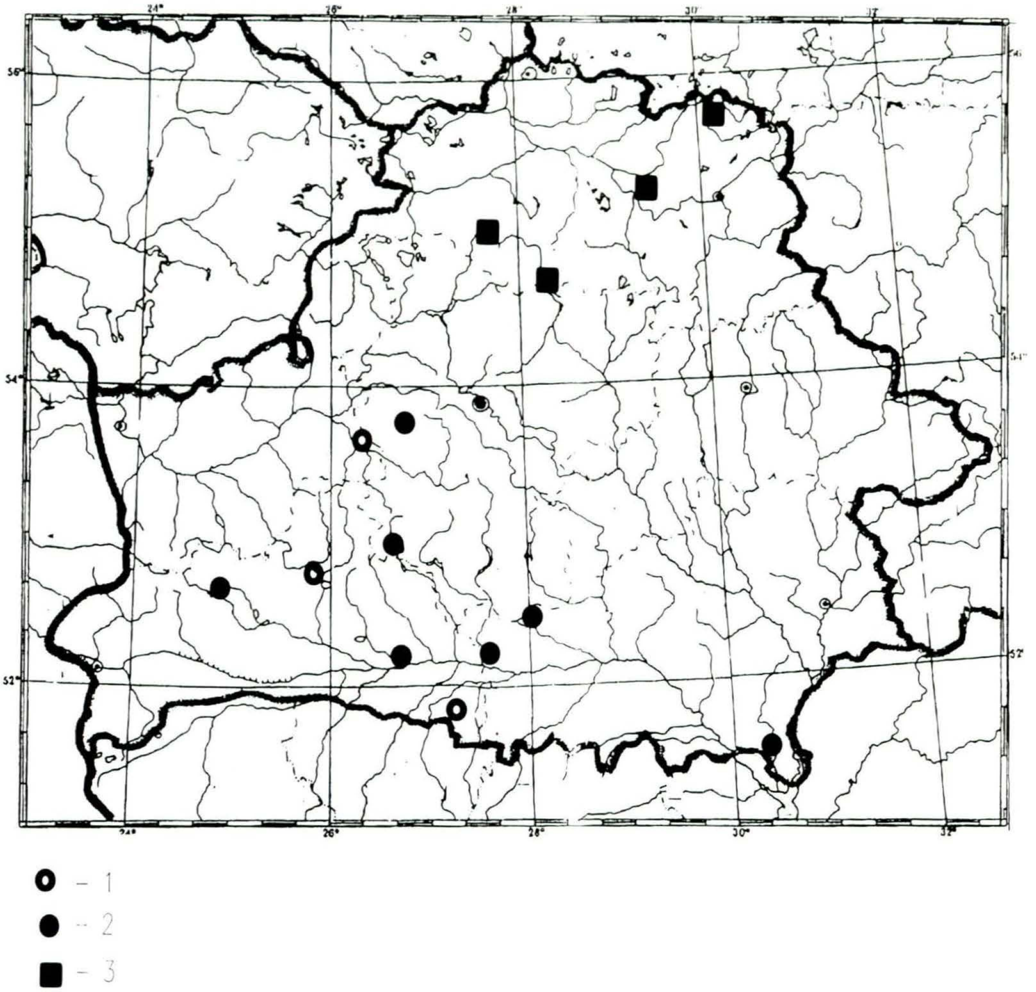

Figure 1. — *Main sampling sites in dietary studies of* Strix *owls in Belarus, samples of no less than 75 prey items were collected in every site. 1 — Great Gray Owl (*Strix nebulosa*). 2 — Tawny Owl (*S. aluco*). 3 — Ural Owl (*S. uralensis*).*

Table 1.—*Diet of Strix owls in Belarus.*

Prey category	**Percent of number of prey items**		
	S. uralensis	***S. aluco***	***S. nebulosa***
Sorex spp.	17.0	17.1	24.9
Other *Insectivora*	6.2	1.9	2.4
Mustelidae	0.2	0.2	0.2
Gliridae	0.2	2.1	-
Muridae	0.8	12.1	0.9
Microtus spp.	37.8	20.8	61.0
Clethrionomys glareolus	24.3	20.2	6.4
Arvicola terrestris	3.6	1.2	4.0
Other *Rodentia*	0.9	0.7	0.2
Birds	3.5	5.2	-
Anurans	3.5	9.3	-
Beetles	2.0	8.3	-
Total number of prey	613	1,517	454

Table 2.—*Complete list of prey species and their occurrence in the diets of* Strix *owls in Belarus.*

Prey Species/type	Percent of number of prey items		
	S. uralensis	*S. aluco*	*S. nebulosa*
Neomys fodiens	4.6	0.9	2.0
Sorex araneus	7.6	5.3	15.7
S. minutus	2.8	3.3	6.6
S. caecutiens	0.3	0.2	-
Sorex spp. *(Araneus + caecutiens)*	6.3	8.3	2.6
Crocidura spp.	-	0.1	-
Talpa europaea	1.6	0.9	0.4
Mustela erminea	0.2	0.1	0.2
M. nivalis	-	0.1	-
Sciurus vulgaris	0.3	-	-
Sicista betulina	0.6	0.7	0.2
Glis glis	-	0.7	-
Dryomys nitedula	-	0.4	-
Muscardinus avellanarius	0.2	1.0	-
Apodemus spp.	0.8	9.7	0.2
Mus musculus	-	0.1	-
Micromys minutus	-	2.0	0.7
Rattus spp.	-	0.3	-
Microtus arvalis/epiroticus	2.9	10.6	0.4
M. agrestis	32.6	4.5	28.7
M. oeconomus	2.3	6.7	31.9
Clethrionomys glareolus	24.3	20.2	6.4
Arvicola terrestris	3.6	1.2	4.0
Bonasa bonasia	0.7	0.1	-
Crex crex	-	0.1	-
Sterna hirundo	-	0.1	-
Columba palumbus	0.3	-	-
Dendrocopus major	-	0.1	-
Riparia riparia	-	0.1	-
Phylloscopus spp.	0.2	0.2	-
Turdus merula	0.2	0.3	-
T. iliacus	0.2	0.1	-
Turdus spp.	0.7	0.5	-
Ficedula hypoleuca	-	0.3	-
Sturnus vulgaris	0.2	0.3	-
Garrulus glandarius	0.2	0.2	-
Certhia familiaris	-	0.2	-
Parus major	-	0.7	-
Parus spp.	0.3	0.9	-
Carduelis flammea	0.2	-	-
C. spinus	-	0.1	-
Carduelis spp.	0.3	0.9	-
Bufo bufo	-	0.1	-
Pelobates fuscus	-	3.0	-
Rana arvalis	-	1.4	-
Rana temporaria	0.8	1.0	-
Brown frog spp.	2.7	2.2	-
Green frog spp.	-	1.6	-
Dytiscus spp.	2.0	1.2	-
Nicrophorus humator	-	0.1	-
Silpha spp.	-	0.1	-
Geotrupes spp.	-	1.8	-
Melolontha spp.	-	3.8	-
Polyphila fullo	-	0.7	-
Prionis coriarius	-	0.5	-
Saperda carcharias	-	0.1	-
	N = 613	N = 1517	N = 454

species prey upon a wider variety of prey. The diet of Tawny Owls is especially diverse, and the importance of six trophic categories approaches or exceeds 10 percent. Ural Owls prey upon as many prey categories as Tawny Owls, but their diet is closer to great grays than to tawnies (table 4); prey categories other than voles and shrews comprise only ca. 10 percent of the Ural Owls' diet.

The use of insects by Tawny Owls and preference for heavier *Microtus oeconomus* Pall. by Great Gray Owls are reflected by the difference in mean prey mass (table 3). However, mean weights of vertebrate prey correlate with predator size (table 3). The gradient of prey specialization from Tawny to Great Gray Owls is also supported by the number of prey species and niche breadth indices (table 3).

Table 5 represents the diet and niche statistics from a pair of neighboring Tawny and Great Gray Owl nests (internest distance was 900 m). Both species had specialized diets, with Great Gray Owls emphasizing the use of bank voles (*Clethrionomys glareolus* Schreber) (compare tables 1 and 2). Common prey categories, excluding bank voles, were used in similar proportions (table 5). Niche breadth for each species was wider and diet overlap between them was smaller (0.382) than for pooled diet data (see tables 3, 4, and 5).

Table 4.—*Food niche overlap between* Strix *owls in Belarus (prey species level).*

	S. uralensis	***S. aluco***	***S. nebulosa***
S. uralensis		0.633	0.667
S. aluco			0.448

Table 5.—*Diet of two* Strix *species in neighboring nests, April-May 1995, Svyatitsa study area, Liahavichi District, Belarus.*

Prey category	**Percent of number of prey items**	
	S. aluco	***S. nebulosa***
Sorex spp.	15.2	16.7
Neomys fodiens	2.2	-
Sicista betulina	10.9	-
Apodemus spp.	8.7	-
Microtus spp.	28.3	26.1
Clethrionomys glareolus [1]	6.5	54.2
Arvicola errestris	2.2	4.2
Birds [2]	17.1	-
Frogs	4.3	-
Beetles	4.3	-
Total prey	46	24
Food niche breadth (species level)	14.21	7.04

[1] Chi-square test, $P < 0.001$

[2] Chi-square test, $P < 0.01$

DISCUSSION

Pooled diet data from different Belarus localities, years, and in part, seasons, were compared with generalized data in Cramp (1985), Marti *et al.* (1993), and Mikkola (1983). All three owl species had a rather specialized diet compared to other European studies. The diet of Belarusian Ural Owls differed considerably from Fenno-Scandian birds with respect to water vole (*Arvicola terrestris* L.) and shrew proportions. Ural Owls in Central Europe ate more mice and fewer shrews than Belarusian birds (Mikkola 1983). The proportions of water voles and shrews in the diet affect mean prey size and prey/predator mass ratio, which in

Table 3.—*Main food niche indices of* Strix *owls in Belarus.*

Niche statistics	***S. uralensis***	***S. aluco***	***S. nebulosa***
Geometric mean weight of prey	22.1[1]	15.4[1,2]	25.3[2]
Mean prey weight — SD	49.6	27.4	25.5
Prey/Predator mass ration, percent (%)	2.7	3.5	2.5
Minimal number of prey species	29	51	13
Food niche breadth (species level)	5.48	12.96	4.55

[1] Mann-Whitney test, $P < 0.05$

[2] Mann-Whitney test, $P < 0.01$

Belarus are about one-half the values reported elsewhere (Marti *et al.* 1993). Tawny Owls have an extremely diverse diet; maximal niche breadth reported for this species was 10.4 (Marti *et al.* 1993). Main prey proportions reported are for gray and bank voles (18-21 percent, respectively) and mice, anurans, and beetles (8-12 percent) (Cramp 1985, Mikkola 1983). Tawny Owl prey sizes correspond well to other reported values (Marti *et al.* 1993). Great Gray Owls in Belarus ate a relatively high proportion of shrews. Furthermore, the inclusion of root voles accounts for the two-fold increase in Belarusian Great Gray Owl diet niche breadth compared to Fenno-Scandian data (Mikkola 1983, Marti *et al.* 1993).

All three *Strix* species breeding in Belarus represent quite different diets with significant differences in prey category composition, niche breadth, and mean prey size. Dietary overlap correlates inversely with owl species range overlap, i.e., species with wider sympatry have less similar diet. It may reflect the absence of actual dietary competition at present as a result of past competition which shaped recent food niches of these species. This conclusion is preliminary and tentative as present data may be biased by sampling protocol, i.e., uneven geographical, habitat, and seasonal distribution of the samples. Data collection in actual sympatric situations (the same small study area during the same season) are needed for further investigation of food resource partitioning between these congeneric species.

Surprisingly, the only available data of this kind (with small sample sizes of prey animals) suggests that competition is important. Significant differences in the proportion of bank vole use, and switching of Tawny Owls from this preferred prey (Cramp 1985, Mikkola 1983) to others not used by potential competitors foraging nearby, may be attributed to Tawny Owls being excluded from the better hunting habitats by territorial and larger Great Gray Owls.

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LITERATURE CITED

Cramp, S. 1985. Birds of the Western Palearctic. Vol 4. Oxford, UK: Oxford University Press. 960 p.

Fedyushin, A.V.; Dolbik, M.S. 1967. Birds of Byelorussia. Minsk: Navuka i Techika. 519 p. (In Russian).

Görner, M.; Hackethal, H. 1988. Säugetire Europas. Leupzig - Radebeul: Neumann. 371 p.

Jaksic, F.M. 1988. Trophic structure of some Nearctic, Neotropical and Palearctic owl assemblages: potential roles of diet opportunism, interspecific interference and resource depression. Journal of Raptor Research. 22: 44-52.

Jaksic, F.M.; Delibes, M. 1987. A comparative analysis of food-niche relationships and trophic guild structure in two assemblages of vertebrate predators differing in species richness: causes, correlations and consequences. Oecologia. 71: 461-472.

Jedrzejewski, V.; Jedrzejewska, B.; Szymura, A. 1989. Food niche overlaps in a winter community of predators in the Bialowieza Primeval Forest, Poland. Acta Theriologica. 34: 487-496.

Herrera, C.M.; Hiraldo, F. 1976. Food-niche and trophic relationships among European owls. Ornis Scandinavica. 7: 29-41.

Lundberg, A. 1980. Why are the Ural Owl (*Strix uralensis*) and the Tawny Owl (*S. aluco*) parapatric in Scandinavia. Ornis Scandinavica. 11: 116-120.

Mikkola, H. 1983. Owls of Europe. London: T & AD Poyser. 397 p.

Marti, C.D.; Korpimäki, E.; Jaksic, F.M. 1993. Trophic structure of raptor communities: a three-continent comparison and synthesis. In: Power, D.M., ed. Current ornithology. New York, NY: Plenum Press: 47-136.

Puzek, Z., ed. 1981. Key to vertebrates of Poland. Mammals. Warszawa: PWN. 367 p.

Strategies for Protecting Western Burrowing Owls (*Speotyto cunicularia hypugaea*) from Human Activities

Lynne A. Trulio[1]

Abstract.—Practitioners have been using numerous methods to protect Burrowing Owls (*Speotyto cunicularia hypugaea*) affected by human activities. Primary approaches include protecting birds and burrows in place, allowing birds to relocate within their nesting territory, allowing birds to colonize new patches, moving birds within the geographic region and moving birds outside the geographic region. Very little data are readily available on most of these. Preliminary information indicates that methods which keep birds near nest burrows may be more successful than those in which birds are relocated outside nesting territories. Adequate monitoring is necessary when using these methods and more data are required to ascertain which conditions will produce successful breeding populations.

The Western Burrowing Owl (*Speotyto cunicularia hypugaea*) is a semi-fossorial bird of the short-grass prairie which nests in burrows dug by other animals such as prairie dogs (*Cynomys* sp.), ground squirrels (*Spermophilus* sp.) and badgers (*Taxidea taxus*) (Haug *et al.* 1993). Owls are migratory throughout much of their range, but occur year round in central and southern California and south Arizona, New Mexico, and Texas. Burrowing Owls are very site tenacious and are not easily forced to move to a different burrow during the nesting season. Burrow fidelity is a widely recognized trait of Burrowing Owls, with owls reusing burrows from 1 year to the next (Green 1983, Martin 1973, Wedgwood 1976). Green (1983) found an average of 76 percent of burrows were reoccupied the next year. At a study site in northern California, an average of 73 percent of nest burrows or burrows within 100 m were reoccupied the next year over a 3 year time span (Trulio 1994).

This species is declining throughout much of its western North American range. It is endangered in Minnesota, Iowa, and throughout its distribution in Canada; it is a species of concern in six other western U.S. States. The extensive destruction of prairie dogs and ground squirrels, the use of pesticides and herbicides, and the conversion of grasslands to agriculture and urban uses have all resulted in this decline (Haug *et al.* 1993, Zarn 1974).

In California, recent research indicates that the Burrowing Owl population has declined by approximately 50 percent in the last 10 years (DeSante and Ruhlen 1995). One reason for this rapid decline is loss of habitat to human uses, especially urban development (DeSante and Ruhlen 1995, Trulio 1995). From a regulatory standpoint, the birds themselves are protected year round and nest burrows cannot be legally disturbed during the nesting season. Owl habitat can be legally destroyed outside nesting season, although compensation for this loss may be required. Numerous laws, including state and federal endangered species acts and environmental impact assessment laws, require mitigation for the destruction of Burrowing Owl habitat. A variety of approaches are being used in an attempt to protect owl populations from decline in the face of disturbance and destruction of their habitat.

Five common protection methods are: (1) protecting existing habitat, especially nest burrows, in place, (2) evicting owls and allowing them to move to a new burrow within their nest territory (passive relocation) (Trulio 1995), (3) allowing owls to move to newly created habitat patches, (4) actively moving birds to new burrows outside their nesting territory but within their geographic region (active relocation), and (5) actively moving birds to new burrows outside their geographic region into areas formerly occupied by Burrowing Owls (reintroduction).

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Very little data exist in the published literature on most of these methods. This paper presents published information as well as preliminary data collected from researchers and consultants belonging to the California Burrowing Owl Consortium, an ad hoc group of researchers, consultants, agency personnel and citizens who are working to preserve Burrowing Owls in California. These data are far from complete, but they provide some indication of the effectiveness of the various methods. Important research needs for each method are identified.

RESULTS AND DISCUSSION

Protect in Place

Given the site tenacity and burrow fidelity of Burrowing Owls, this method is expected to be successful in protecting birds if disturbances are kept far enough away from occupied burrows. Protecting habitat in place allows birds to remain at the burrows they have chosen and also allows them to return to preferred sites in subsequent years. However, habitat protected in place may become surrounded by lands converted to human uses which may be detrimental to owl habitat quality.

Currently, no published information exists on protecting owls and their habitat in place on disturbance or development sites. No cases had been collected from Consortium members by the time this paper was submitted. To assess this method, results on the long-term use of protected burrows are needed, as are data on the effects of different adjacent land uses and habitat fragmentation on burrows. Burrowing Owls are somewhat tolerant of human activity and development (Trulio 1994, Weseman and Rowe 1987), but the maximum level of activity that will still allow long-term persistence of owls on a site must be determined.

Passive Relocation

Passive relocations are those in which owls are evicted from their occupied burrows. Owls are not allowed to return to the burrows from which they are evicted and they must choose a new burrow. Typically, artificial burrows are constructed as near to the eviction burrows as possible to provide acceptable unoccupied burrows for owl use. Data from six passive relocations in northern California were presented in Trulio (1995). Artificial burrows were created in each case and two to six owls were evicted from their original burrow. In five of the six cases, the artificial burrows were immediately occupied. In only one of these cases were the evicted owls banded and they were known to have moved into the artificial burrow created for them. That burrow supported successfully breeding birds for 3 consecutive years. In the other four cases the evicted owls were not banded and it is not certain they were the birds occupying the new burrows.

New burrows which were used by birds were within 75 m of the eviction site. In one of the six cases the new burrows were not used; those burrows had been placed 165 m from the original burrow. Results from an additional passive relocation in 1995 showed that the evicted birds did not occupy the new artificial burrows; these were 136 m from the eviction site. Researchers have found that the area of greatest activity around owl nest burrows extends from approximately 50 to 100 m from the burrow (Haug and Oliphant 1990, Thomsen 1971). Owls readily explore burrows within this radius. Placing artificial burrows more than 100 m from the eviction burrow may greatly reduce the chances that evicted birds will find the new burrows.

The rates of survival and reproduction of owls evicted to artificial burrows is not known. The long-term use of artificial burrows and the ability of these burrows to maintain populations requires study. Important questions relative to this method are: (1) What burrow conditions are most attractive to owls? (2) What is the greatest distance artificial burrows can be located from eviction burrows for owls to occupy them? (3) What is the reproductive rate of owls moving to artificial burrows? (4) Do owls use artificial burrows on a long-term basis?

New Habitat Patches

Creation of new habitat patches near occupied areas may provide increased areas for birds to colonize. This method for preserving population size has not yet been used on a regular basis to protect owl groups. In northern

California, a new habitat patch in the City of Palo Alto has recently been colonized by at least three pairs of owls. The site is a newly closed landfill with a healthy ground squirrel population. This new habitat patch is approximately 1 km from other occupied owl habitat. Creating new patches to protect or increase owl populations may become an attractive approach to mitigating for impacts to owl populations.

Conditions that may attract owls to new sites and facilitate owl dispersal to those sites are not well known. Prairie dog colonies may provide a model for conditions, such as distance between patches, which could result in the successful use of new habitat areas. In natural midwestern habitats, Burrowing Owls lived in the patchy habitat created by prairie dogs. Flath and Clark (1986) studied historic prairie dog colonies in Wyoming and found that the distances between patches occupied by the rodents in two "dog towns" averaged 2.9 km and 3.4 km. Groves and Clark (1986) measured an extant colony and found patches occupied by rodents were an average of 0.92 km apart. If prairie dog colonies are used as a model for spacing owl habitat, then newly created patches should not be more than about 3 km from an occupied owl colony. Habitat requirements, patch spacing, and proper habitat management are just a few of the many issues associated with this method that require research.

Active Relocation

A third method, active relocation, requires that birds be captured and moved to new burrows outside their nesting territory, but within the local range occupied by Burrowing Owls. Typically, temporary aviaries are placed over the new artificial burrows for some time (hacking), usually several weeks, then the aviaries are removed (Trulio 1995). Many active relocations have been conducted in California, often to move birds off sites which will be disturbed or developed. Much of the information on this method is in consultant reports and is not readily available. Information collected to date from Consortium members is presented in table 1.

Table 1.—*Information on active Burrowing Owl (*Speotyto cunicularia hypugaea*) relocations in northern California.*

Original site (City)	**Number moved**	**Distance moved**	**Fate of birds**
Santa Clara[1]	10 birds	30 km	• 2 birds bred successfully; in year 2, male stayed, was at site, but female had disappeared • 2 bred but nest was destroyed by predator; that season, male disappeared, female flew back to original location • 2 stayed one breeding season; female flew back to original location and male disappeared • 2 disappeared within 10 days of release; 4 birds, total, ultimately disappeared • 1 killed by predator • 1 flew immediately back to original site; 3 birds, total, ultimately returned to original site
Santa Clara	4 birds	0.8 km	• 2 disappeared that season • 2 flew back to original site
Winters[2]	7 birds	24+ km	• 7 disappeared within 1 year
Oakland[3]	4 birds	0.8 km	• 2 disappeared that season • 2 flew back to original site
Oakland[3]	2 birds	0.8 km	• 2 disappeared that season

[1] H. T. Harvey and Associates (1993).

[2] T. Schulz, pers. comm.

[3] L. Feeny, pers. comm.

Although incomplete, this list gives some preliminary results on the effectiveness of the method. Of the 27 birds relocated to new burrows, 17 disappeared (63 percent) within a year of release. One of these bred at the new site, but the nest was destroyed by predators. Seven birds (26 percent) flew back to their original site. Two bred successfully on site (7 percent). Two bred unsuccessfully (7 percent). One was a victim of predation (4 percent) and one stayed on the site for two breeding seasons (4 percent). The strong site tenacity of the birds is an obvious explanation for why many owls returned to their original location. The fate of most relocated owls is unknown as the majority disappeared.

These projects did not result in the retention of the majority of relocated birds on site as successfully breeding pairs. However, there may be circumstances under which active relocation may be successful. For example, two pairs of birds from the first Santa Clara relocation did breed on site the year they were moved there. More work to determine under what conditions birds will stay and reproduce at new sites is needed. Research on what conditions constitute good habitat, especially prey base needs and predator pressure limits, is very important. Our ability to find or establish good to excellent habitat is central to the success of this method, as well as for the patch creation and reintroduction methods.

Reintroduction

Reintroduction, another important type of relocation, generally requires moving animals long distances, well beyond their territory and the local geographic region, to parts of their range which they formerly occupied. This method has not yet been used to move birds from urbanizing areas, but it could be an attractive option if it is successful.

Three large scale reintroductions have been undertaken in Manitoba (De Smet 1997), Minnesota (Martell *et al.* 1994), and British Columbia (Dyer 1988). De Smet (1997) reported that 169 young and 85 adults were captured in South Dakota and released into temporary aviaries and artificial burrows in Manitoba. After release from the aviaries, only one of these birds, a juvenile, was seen the next year. Martell *et al.* (1994) reintroduced 104 fledgling owls from South Dakota to hack sites in Minnesota, distances of 450 and 600 km away. None of these birds were seen after the summer they were released. Beginning in 1983, owl families were relocated to British Columbia from Washington state. After over a decade of work, Dyer (pers. comm.) states that the program has not successfully established a self-sustaining population and new approaches to restoring the species are being attempted.

CONCLUSION

Various methods to preserve Burrowing Owl populations are being implemented. These techniques range from protection in place to long distance reintroductions. Very little information is easily available on the value of any of these methods for preserving owls affected by human activities. The preliminary data presented here suggest that keeping birds near their chosen nest territory and allowing them to chose their own burrows may be more successful than physically relocating birds to new sites. It is critical that projects employing techniques to protect owls from human activities be adequately monitored to determine their short and long-term effectiveness. Research is required on the conditions under which different methods may result in the preservation of breeding populations.

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LITERATURE CITED

DeSante, D.F.; Ruhlen, E. 1995. A census of Burrowing Owls in California, 1991-1993. Point Reyes Station, CA: Institute for Bird Populations.

De Smet, K. 1997. Burrowing Owl (*Speotyto cunicularia*) Monitoring and Management Activities in Manitoba, 1987-1996. In: Duncan, J.R.; Johnson, D.H.; Nicholls, T.H., eds. Biology and conservation of owls of the northern hemisphere: 2d international symposium; 1997 February 5-9; Winnipeg, Manitoba. Gen. Tech. Rep. NC-190. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station: 123-130.

Dyer, O. 1988. Reintroductions of Burrowing Owls (*Athene cunicularia*) to the south Okanagan Valley, British Columbia (1983-1988). Report to the Ministry of Environment, British Columbia. 7 p.

Flath, D.L; Clark, T.W. 1986. Historic status of black-footed ferret habitat in Montana. Great Basin Naturalist Memoirs. 8: 63-71.

Haug, E.A.; Millsap, B.A.; Martell, M.S. 1993. Burrowing Owl. The Birds of North America. 61: 1-19.

Haug, E.A.; Oliphant, L.W. 1990. Movements, activity patterns, and habitat use of Burrowing Owls in Saskatchewan. Journal of Wildlife Management. 54: 27-35.

Harvey, H.T., and Associates. 1993. Environmental impact report on the Burrowing Owl, Interland-Mission College Development. EIR Supplement Mercado Santa Clara and Mission College Office Development. 55 p.

Green, G.A. 1983. Ecology of breeding Burrowing Owls in the Columbia basin, Oregon. Corvallis, OR: Oregon State University. 51 p. M.S. thesis.

Groves, C.R.; Clark, T.W. 1986. Determining minimum population size for recovery of the black-footed ferret. Great Basin Naturalist Memoirs. 8: 150-159.

Martell, M.; Tordoff, H.B.; Redig, P.T. 1994. The introduction of three native raptors into the midwestern United States. Raptor Conservation Today. 465-470.

Martin, D.J. 1973. Selected aspects of Burrowing Owl ecology and behavior. Condor. 75: 446-456.

Thomsen, L. 1971. Behavior and ecology of Burrowing Owls on the Oakland Municipal Airport. Condor. 73: 177-192.

Trulio, L.A. 1994. Study of the status, ecology and distribution of Western Burrowing Owls at Naval Air Station, Moffett Field Santa Clara County, California. Contract nr N62474-91-M-0603. 21 p. Sponsored by Department of the Navy, Naval Air Station, Moffett Field, CA.

Trulio, L.A. 1995. Passive relocation: a method to preserve Burrowing Owls on disturbed sites. Journal of Field Ornithology. 66: 99-106.

Wedgwood, J.A. 1976. Burrowing Owls in south-central Saskatchewan. Blue Jay. 34: 26-44.

Wesemann, T.; Rowe, M. 1987. Factors influencing the distribution and abundance of Burrowing Owls in Cape Coral, Florida. In: Adams, W.; Leedy, D.L., eds. Integrating man and nature in the metropolitan environment, proceedings of the 1986 national symposium on urban wildlife; 1986 November 4-7; Chevy Chase, MD. Columbia, MD: National Institute for Urban Wildlife: 129-137.

Zarn, M. 1974. Burrowing Owl. Tech. Note T-N-250. Denver CO: U.S. Department of Interior, Bureau of Land Management. 25 p.

Flammulated Owl (*Otus flammeolus*) Population and Habitat Inventory at its Northern Range Limit in the Southern Interior of British Columbia

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Abstract.—Flammulated Owl (*Otus flammeolus*) ecology at the northern limit of its range (southern interior of British Columbia) necessitates that inventory data include replicated sampling throughout and between breeding seasons for accurate population and habitat assessment. Auditory census and nest surveys must be linked to assess habitat suitability; census alone can only indicate habitat capability through documentation of presence or absence of Flammulated Owls. Standardization of comprehensive census and nest surveys can provide multi-year population data for landscape management plans. Trend data may serve as a measure of recruitment and help to identify source habitats for retention in management plans.

The Flammulated Owl (*Otus flammeolus*) is a neotropical migrant that nests in cavities in the montane Douglas-fir (*Psuedotsuga menziesii*) forests of western North America (McCallum 1994, Reynolds and Linkhart 1987a, Cannings 1982). Prior to 1989, little was known about the habitat requirements of the insectivorous owl in the southern interior of British Columbia, at the species' northern range. Incidental surveys had revealed the presence and absence of Flammulated Owls in the southern interior of the Province, and historical records indicated Wheeler Mountain, near Kamloops, B.C. (fig. 1), may have had a higher number of nesting pairs of owls than surrounding areas (Howie and Ritcey 1987).

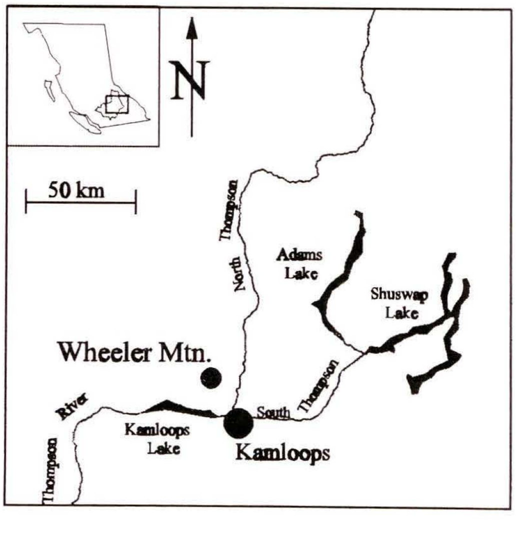

Figure 1.—*Wheeler Mountain near Kamloops, British Columbia.*

Habitat research began on Wheeler Mountain in 1989, necessitated by a logging moratorium for the area. The objective was to investigate critical nesting and foraging habitat features to develop integrated management prescriptions. By the early 1990's, the decision was made by the B.C. Ministry of Environment, Lands and Parks and the B.C. Forest Service to defer logging on Wheeler Mountain. The area has since been officially set aside for preservation as part of a Protected Area by the Kamloops Land and Resource Management Planning (LRMP) Team (1995), proclaimed by British Columbia Provincial Government. Habitat research has expanded to include post-fledging studies and the development of a predictive model to assist managers with Flammulated Owl habitat inventory in the southern interior of B.C.

Multi-year data from Wheeler Mountain (1989-1991, 1994-1996) was used to assess the accuracy of auditory census and nest site survey techniques as management tools for habitat assessments. Results indicated that auditory census inventory techniques can only be used to determine presence or absence of owls in an area and should be replicated to confirm habitat capability. Nest surveys must be conducted to estimate habitat suitability and a standardized procedure that includes auditory census can be used to estimate relative nesting density. The long-term results clearly indicate the necessity for standardized, comprehensive inventory techniques and their appropriate selection to accurately meet informational requirements of integrated management.

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STUDY SITES

Wheeler Mountain (fig. 1) was the principle study site and is a 1,600 ha area approximately 10 km north of the City of Kamloops, on the west side of Lac du Bois (50°46' N and 120°28' W). Elevation ranges from 850 to 1,200 m with slopes to 75 percent. Forest cover is classified as interior Douglas-fir biogeoclimatic zone, specifically IDFxh2—the Thompson very dry hot interior Douglas-fir variant (Lloyd *et al.* 1990). Wheeler Mountain is surrounded by grassland on the east and south aspects and continuous Douglas-fir and ponderosa pine (*Pinus ponderosa*) forest on the north and west aspects, respectively.

Forests on the mountain are mature to old-growth (80-200+ years). Forest cover at the top of the mountain is highly fragmented by cliffs and rock. Douglas-fir is the climax species dominating the study site with ponderosa pine occurring as a subdominant in sub-xeric to xeric sites. Ponderosa pine component has been reduced by fire suppression and previous selective timber harvests 25-35 years ago (D. Low, B.C. Ministry of Environment, Lands and Parks, pers. comm.). Fire suppression has resulted from British Columbia Forest Service policy (Watts 1983) as well as reduced understory fuel loading caused by cattle grazing (D. Low, Ministry of Environment, Lands and Parks, pers. comm.). The absence of fire has encouraged Douglas-fir regeneration in the form of dense thickets. The stem density of these thickets has led to stagnant stands with recurring outbreaks of western spruce budworm (*Choristoneura occidentalis*); budworm damage is extensive in mesic sites (van Woudenberg 1992).

The predominant understory species include saskatoon (*Amelanchier alnifolia*), birch-leaved spirea (*Spirea betulifolia*), common snowberry (*Symphoricarpos albus*), soopolallie (*Shepherdia canadensis*), kinnickinnick (*Arctostaphylos uva-ursi*), pinegrass (*Calamagrostis rubescens)*, bluebunch wheatgrass (*Agropyron spicatum*), and rough fescue (*Festuca scabrella*). Mesic sites tend to be dominated by pine grass and rough fescue with variable amounts of shrubs. Bluebunch wheatgrass dominates xeric and south aspect sites, also with a variable shrub layer; common juniper (*Juniperus communis*) occupies the shrub layer at low elevations. The bryophyte layer is sparse in both mesic and xeric sites.

The mean annual precipitation for the area is 37.5 cm with maximum precipitation occurring in spring (May and June) and winter (December and January) (Mitchell and Green 1981). Mean annual temperature is -5°C, mean July temperature is 16°C and a frost free period of 90 days.

The additional study sites surveyed in 1996 that immediately surround Wheeler Mountain include the Tranquille Valley and Red Plateau. The Tranquille River Valley runs north-south between Red Plateau on its west flank and Wheeler Mountain on its east. Skull Mountain is approximately 70 km north of the City of Kamloops, near the town of Barriere and is located on the west side of the North Thompson River. Habitats sampled in the additional study sites in 1996 were of the same elevational range, forest cover type and structure and biogeoclimatic variant as Wheeler Mountain.

METHODS

A standardized, auditory census methodology was first developed in 1989 and improved with multi-year results. Based on census techniques initially used by Howie and Ritcey (1987), census stations were established at 500 m intervals. Established roads or reconnaissance lines through a stand served as transects. On Wheeler Mountain, the entire main road (18 km) was sampled in 1989-1991, and 1994-1996. The road traversed Flammulated Owl habitat across the entire area at mid-slope, providing an optimal cross-section of the site's habitat. The same people surveyed Wheeler Mountain for several years, suggesting that bias in the numbers of birds detected from year to year was reasonably controlled.

Auditory census began at dusk and often continued until dawn. Ten minutes were spent at each census station along a transect to record any birds calling spontaneously. If no birds were detected, the territorial or advertisement call was mimicked by the observer for an additional 5 minutes to induce a response. Mimicking calls was found to be more effective to induce a response than playback tapes; sampling was conducted by observers who were capable of reproducing a call that could induce a response from a Flammulated Owl. The bearing of the call and estimated distance to the owl based on the strength of the call were recorded. The variability associated with the bearing of an owl call was quantified using discrete confidence intervals of plus or minus 0, 15, 30, or 60 degrees. Distances were estimated based on the strength of the call which was determined by the number of notes detected in each vocalization of a calling series. For example, at large distances (> 200 m), the typical two-noted hoot was commonly detected as one quiet note; at very close proximity—within a few meters—two notes with an intervening rasp (sometimes referred to as the three-note call) was detected. Interference from background noise, such as wind or running water, and influence of terrain and forest cover were considered in distance estimates. Visual detections of calling birds by census takers provided experience with estimating distances.

Census results were applied to a standardized method for nest site searches to estimate the relative nesting density of owls. For 1995-1996 data, the locations of all census stations along a transect were recorded using a hand-held GPS (Global Positioning System) and compass bearings to calling owls were mapped using a GIS (Geographic Information System). Triangulation of the bearings assisted nest site surveys by identifying areas used by calling owls (e.g., potential home range locations) and therefore the vicinity of nest sites. Nest site surveys were conducted along parallel transects 50 m apart that traversed areas where owls were detected during census efforts. Auditory censes were conducted between mid-May and early June and nest site searches were conducted during the months of June and early July, beginning with xeric sites. Surveys conducted on Wheeler Mountain were expanded to include the Tranquille Valley, Red Plateau, and Skull Mountain in 1996.

Aerial photographs were used in support of nest site surveys. Flammulated Owl nesting and foraging habitat areas investigated on Wheeler Mountain typically had a distinct forest cover texture that could be recognized on aerial photographs. Areas displaying the characteristic texture were delineated on 1:15,840 air photos and overlaid with nest site survey transects. Auditory census results did not always include owl detections in all areas of the habitat forest cover texture. Periodically, areas of "non-Flammulated Owl habitat" forest cover texture were surveyed to ensure that nest sites were not being missed and the methodology was accurate. Nest surveys were conducted during the coolest part the of day—early in the morning. Nest sites were confirmed by locating a female Flammulated Owl at the cavity entrance upon disturbance at the bole of the tree or snag. During the first 3 years of the project, limited resources and research objectives necessitated the same individuals to work both late evenings and full days. Consequently, nest site searching was conducted during the daytime while census work was completed at night.

RESULTS

Auditory Census

During the 1989 nesting season, owls were censused on Wheeler Mountain from 15 May until 20 June. Figure 2 indicates the proportion of the total calls detected at each station. The third week of May was the peak calling period. Overall, calling began to decline by late May; fewer spontaneous calls were detected than induced calls. The fewest numbers of birds were detected 23 May 1989 (on this night temperatures were so low that rain turned to snow between 2300 and 2400 hrs).

Census data results for 23 May in 1995 and 1996 are shown in table 1. The data for 1996 shows the highest numbers of birds recorded.

Nest Site Surveys

Table 2 shows the numbers of nests found on Wheeler Mountain in each year of study since 1989. The numbers of nests found in the first few years of research were consistently lower than the latest years of surveys. The highest number of nests were found in 1995 (14 nests). The fewest nest sites found recently were surveyed in 1996; at least three of the nine nest sites found failed.

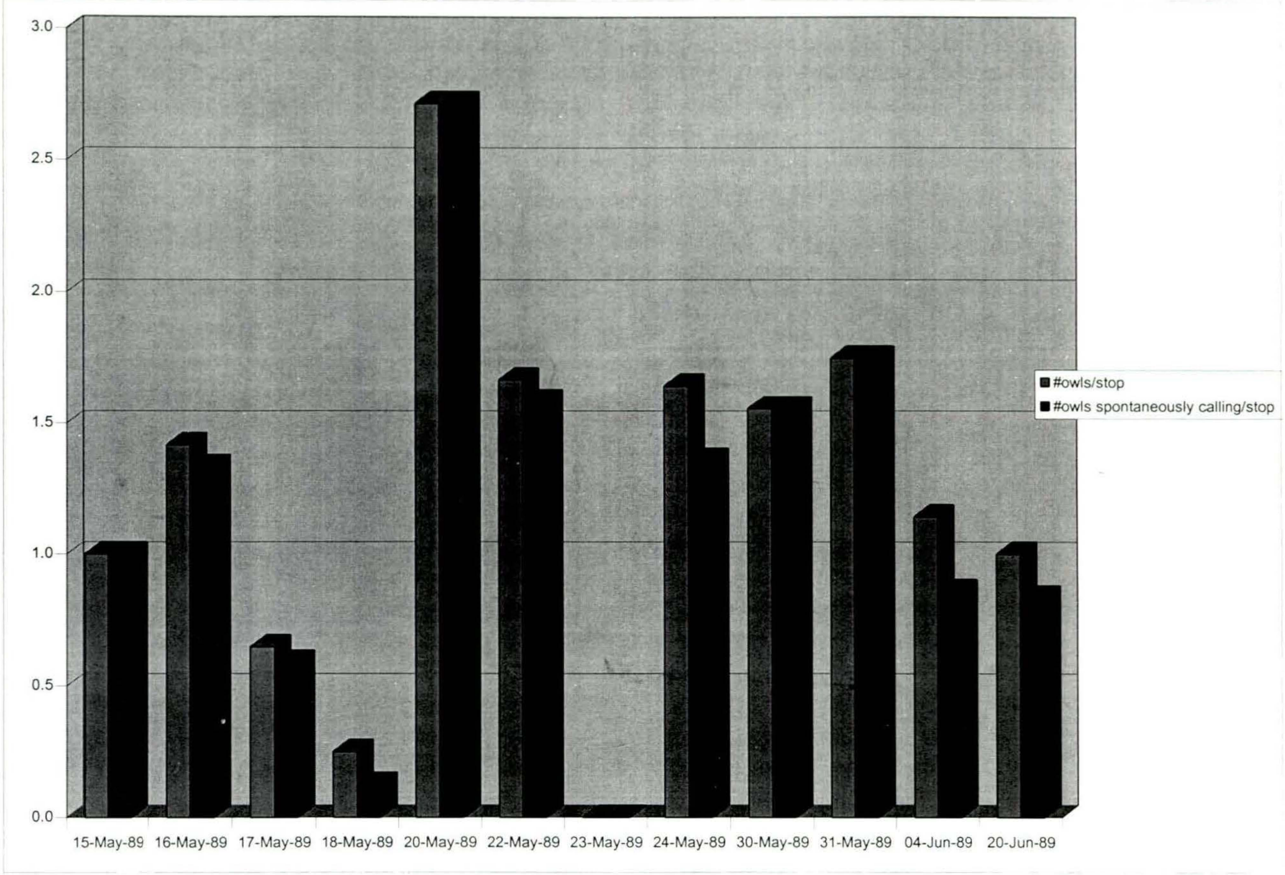

Figure 2.—*Proportion of Flammulated Owls (*Otus flammeolus*) detected per census stop on Wheeler Mountain near Kamloops, British Columbia in 1989.*

Table 1.—*Results of Flammulated Owl (*Otus flammeolus*) 23 May census at Wheeler Mountain near Kamloops, British Columbia for 1995 and 1996.*

	1995	1996
Owl detections/linear km surveyed	3.3	6.2
Mean number birds detected/stop	1.6	3.0
Total number of detections	52	100
Conservative estimate of birds present	26	40

Table 2.—*Flammulated Owl (*Otus flammeolus*) nest sites found on Wheeler Mountain near Kamloops, British Columbia in each year of survey from 1989-1996.*

Year	Number of nest sites detected
1989	3
1990	4
1991	4
1994	12
1995	14
1996	9

Figures 3 and 4 show the overlay of census bearings and nest site locations for 1995 and 1996, respectively. Nest sites were located near or at bearing lines of owl calls recorded during census and also away from bearings, near areas where calling birds were detected. Census transects shown are roads that traversed suitable Flammulated Owl habitat.

Along the main road in the Tranquille Valley, 28 detections were made at 30 census stations sampled between 20 and 21 May 1996; no nest sites were found. In the Tranquille community area, approximately 20 ha near the head of the Tranquille Valley, 29 detections were made at 22 census stations 25 and 28 May. This site was traversed on foot along a B.C. Forest

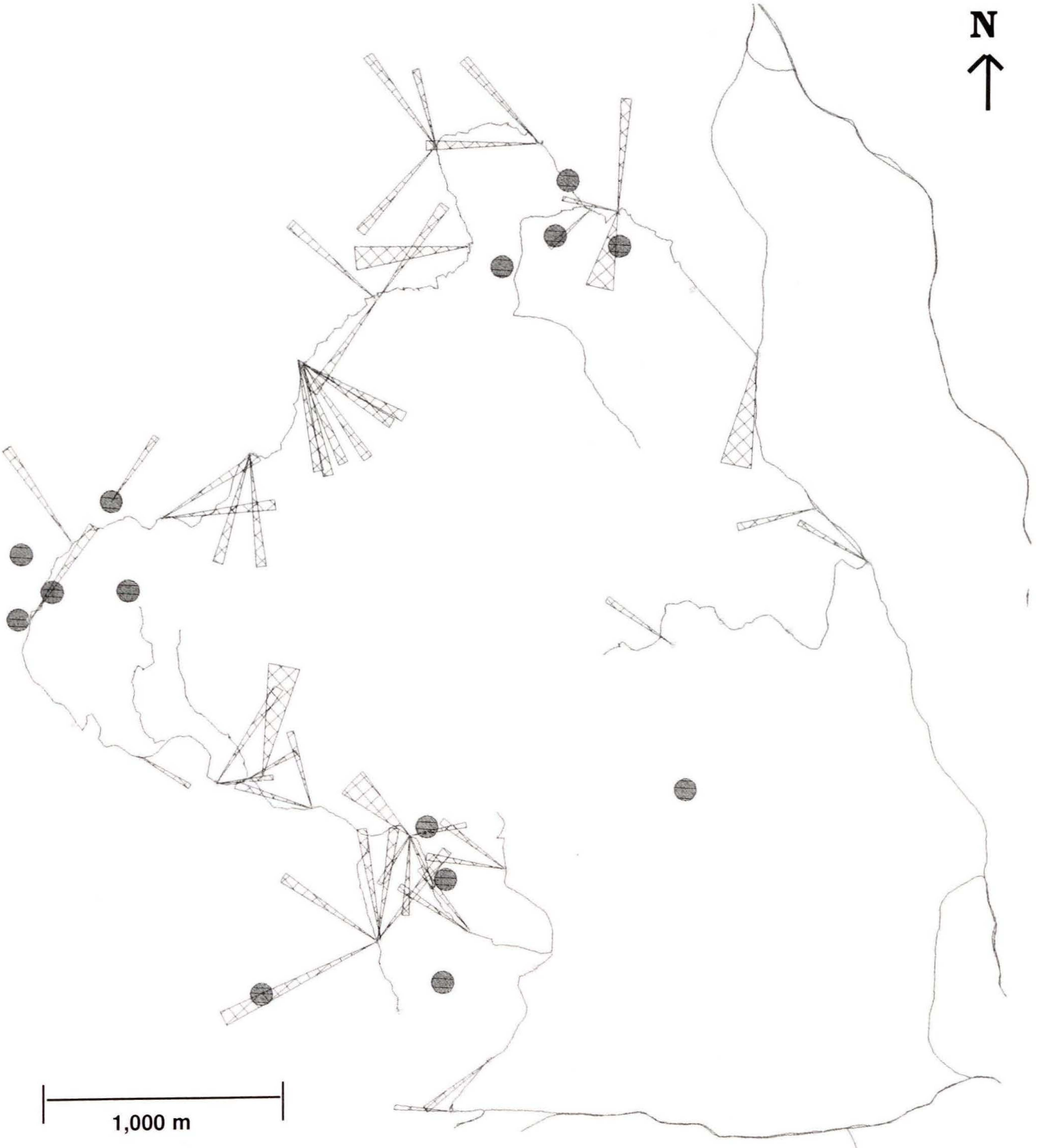

Figure 3.—*Bearings (wedges) of Flammulated Owl (*Otus flammeolus*) calls recorded on 23 May 1995 and nest sites (circles) located in 1995, near Kamloops, British Columbia.*

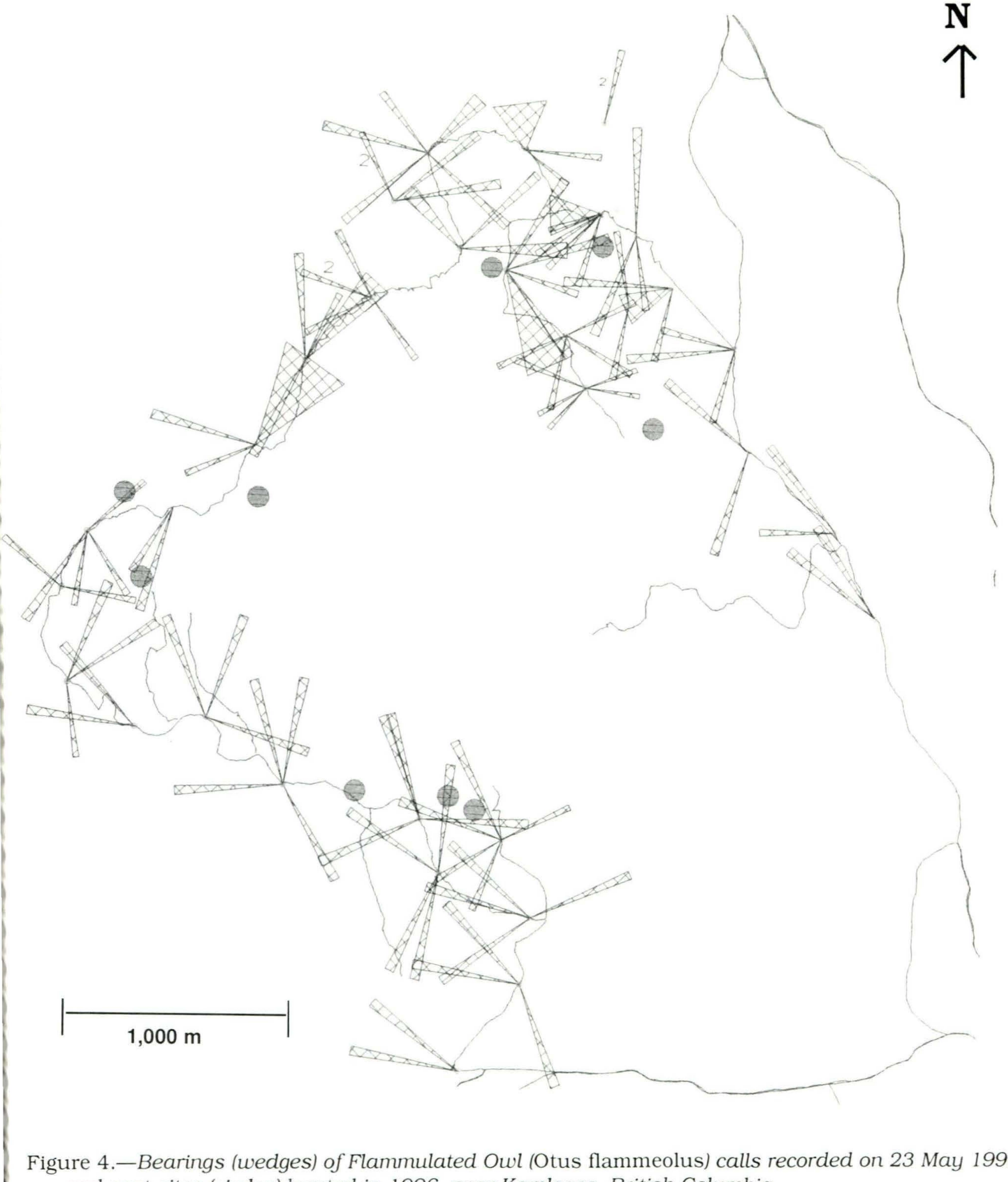

Figure 4.—*Bearings (wedges) of Flammulated Owl (*Otus flammeolus*) calls recorded on 23 May 1996 and nest sites (circles) located in 1996, near Kamloops, British Columbia.*

Service main reconnaissance line with perpendicular secondary lines. At each 100 m interval, bearings of continuous owl calls were recorded, providing detailed information for triangulation which was used to estimate the minimum number of owls present in the area to be seven; one abandoned nest was found (table 3). A transect section of 7.5 km in the Red Plateau area had four nest sites; two nest sites were found in the remaining 15 km of linear transect (table 3).

Table 3.—*Flammulated Owl (*Otus flammeolus*) nest sites per linear km of census transect surveyed in 1996, British Columbia.*

Location	Nest sites/km	Transect length (Linear km sampled)
Wheeler Mountain	0.5	18
Tranquille Valley	0.1	14
(includes Tranquille community area)		
Red Plateau	0.3	13
Skull Mountain	0.2	14

DISCUSSION

The census results for Wheeler Mountain indicate the range of fluctuation in detections of owls within one season and between years (fig. 2, table 1). Depending on the time of the census, new migrant arrivals may be detected among those that are in the process of or have already set up territories and acquired mates. The third week of May is the peak calling period (fig. 2), when migrants have likely saturated the area and territory boundaries are being established and defended. Mimicking a calling owl in mid-May on Wheeler Mountain has often resulted in the individual retreating before responding. At the end of May and early June, Flammulated Owls will respond by moving closer to the observer, presumably to defend their territory by advertising the boundary location.

At the beginning of May, early migrant arrivals will either reclaim territories used in the past (Reynolds and Linkhart 1987b) or begin establishing a new home range, the latter being the owl that may retreat from a mimicked call made by an observer. At the peak calling period, most birds have arrived and are competing for mates and territories. The early migrants that have established territories may or may not be contributing to the calls detected. Males that have a territory but as yet are unmated may be calling to attract females from the latest arrivals. If pairs have formed on territories established early in May, territorial or advertisement calling will be unnecessary except to warn intraspecific intruders. For example, two birds were heard calling on 8 May 1995 from an area where owls have consistently been found on Wheeler Mountain; on 10 May 1995 only one of these birds was heard calling. Further, on 23 May 1995, when the highest number of calls were recorded elsewhere on the mountain (fig. 3), only one bird was heard at this location. Nest surveys located five nests in the area, three of which were directly along the bearings of the calls. The observations suggest that early arrivals may have had established territories and potentially begun nesting activity by the time most migrants were passing through searching for territories and mates. Habitat at sites where nesting begins earliest is likely preferred and may be optimal; if limited to those census results recorded only during peak calling periods, the area with five nests would not have documented, and nest searches relying on these same census results would have failed to detect all the nest sites.

Figures 3 and 4 exemplify the need to replicate surveys of census transects from the time migrants first arrive until nesting is underway so that most calling males can be detected and nest sites are less likely to be missed during nest surveys. The mapped bearings of calls for one evening only in 1995 and 1996, (figs. 3 and 4, respectively) at the peak calling period, illustrate that not all nest sites are located in the vicinity of census bearings or where birds were detected calling. The multi-year results for Wheeler Mountain showed that nests occurred in clusters, relative to total available area, and tended to be located in areas where birds were heard calling. These data suggest productive nesting habitat may have a patchy distribution. Nesting productivity may also be unevenly distributed through time. Xeric, south and east aspect sites that receive more sunlight earlier in the spring than mesic, north and west aspect sites and have warmer temperatures for longer periods throughout the day will likely provide earlier nesting opportunities to Flammulated Owls. South aspect nest sites tended to fledge before north aspect sites, suggesting that south aspect, xeric sites will have territorial males calling sooner and potentially for less time through May than birds in mesic sites. Therefore, triangulation of bearings recorded at multiple auditory surveys beginning in early May, when migrants first arrive, will delineate potential home range sites and indicate patches of productive habitat for nest surveys.

The owl calls plotted for the peak calling periods (figs. 3 and 4) likely represent mate advertisement by new arrivals and territorial boundary displays (Reynolds and Linkhart 1987a). The few calls that have been detected in early May, the bearings of which have often led directly to nest sites, may have resulted from males reclaiming territories used in previous years and advertising for past or new mates from potential nest trees (Reynolds and Linkhart 1987b). By the third week of May, a greater proportion of the calls was likely a result of territory defense and competition, and therefore less indicative of potential nest site locations.

The net result of the peak calling period is likely an abundance of non-nesting individuals passing through the area. In Colorado, Linkhart has found that the majority of calling individuals are territorial (B. Linkhart, pers. comm.). Reynolds and Linkhart (1987b) have also delineated most territories on their study site and report that they tend to all be occupied in most years. The variable number of birds detected calling on Wheeler Mountain from year to year and the differences between numbers of calling birds and nest sites found in the same year suggest one of two possible occurrences: either

1. there is a surplus of non-breeding birds that pass through the area during migration, or
2. the total number of nest sites have never been found and many potential territories remaining unoccupied during most years.

If each calling owl represents one territory, the fluctuations between the numbers of birds detected in census surveys between years would suggest that habitat on Wheeler Mountain is rarely saturated. Furthermore, the disparity between the numbers of nest sites found (tables 2 and 3) and numbers of birds conservatively estimated to be present from census data (table 1), suggests that many territories are occupied by non-nesting birds (in 1996, 31 territories would remain non-nesting). If this were the case, far more birds should be detected calling in June and potentially into July (fig. 2) (see Reynolds and Linkhart 1987a). It would be expected that if all calling birds were territorial, detections might persist for at least a few more nights (fig. 2). Therefore, the fluctuations in numbers of birds heard between years and the extremely short peak in spontaneous calling (fig. 2) suggest that a surplus of non-territorial birds must occur on Wheeler Mountain. It is possible that not all nest sites are detected each year and the survey methodology developed as of late (results shown in table 1) may be improved by expanding nest surveys to include night searches. However, migratory species, particularly passerines, are often recorded in atypical habitats and at large densities en route during migration (R. Howie and D. Low, B.C. Ministry of Environment, Lands and Parks, pers. comm.). Wheeler Mountain may provide preferred habitat for migrants. The combination of security cover and food supply may be optimal for migrants but is likely inadequate to support 1.8 territorial birds/ha (extrapolating linear data from table 1 to the area, 895 ha).

The highest density of Flammulated Owls on Wheeler Mountain was recorded in the coldest and wettest year of research; this strongly suggests that the site is preferred habitat but the numbers of calling birds is not indicative of the numbers of territories present. The only census station where an owl was not detected on Wheeler Mountain (on 23 May 1996) was in an area of some of the poorest habitat on the mountain. The nesting results shown in table 3 suggest a disproportionate selection for habitat on Wheeler Mountain. Although Wheeler Mountain had fewer nests than the previous year, it retained the highest nesting density compared with surrounding areas. Replicated census and nest site surveys in the surrounding areas in subsequent years are necessary to quantify habitat preference.

Fewer calls were detected later in the breeding season, near the end of June (fig. 2) when nesting activity had begun. In particular, spontaneous calling dropped off. Mate advertisement and intraspecific territory defense were no longer necessary. If similar numbers of birds are calling in an area as late as July, critical nesting habitat features are likely absent and the habitat is unsuitable, or marginal at best, for nesting owls. Reynolds and

Linkhart (1987a) found that few birds called on their study site spontaneously in July and those that did were confirmed to be unmated males. Conversely, in stands of productive owl habitat, territorial male owls may call only a few nights or couple of weeks after they arrive at the site. Particularly if a warm spring produces an abundance of insects, experienced pairs of owls familiar with a breeding home range may begin nesting activity shortly after they return. The male will stop, or markedly reduce calling once he has attracted his mate. van Horne (1983) suggests that non-breeding adults that comprise the surplus of a population may occupy marginal habitats at higher densities than breeding adults in high quality habitats.

The multi-year results suggest that behavioral characteristics in combination with environmental factors, such as climate, can reduce the accuracy of census results, necessitating that auditory census be replicated within a season. Census data may be useful to indicate habitat capability, but cannot be used to assess habitat suitability. The successive years of census data for the evening of 23 May (fig. 2, table 1) clearly show that censes must be replicated between as well as within seasons to determine habitat capability. No owls were detected 23 May 1989 due to adverse weather conditions. At the same site in 1995 and 1996, an average 1.6 and 3 owls, respectively, were detected 23 May.

The inherent error in the census technique compounds the limitations of the methodology. Flammulated Owls have a ventriloquial call and many of their habitats in British Columbia have variable topography that can contribute to errors in identifying call locations. New arrivals move around a great deal, which the census techniques can encourage so that the same individual may be recorded calling spontaneously at more than one census station. Background noise can be significant, reducing an observer's ability to detect calling owls and accurately identify the species.

The extreme cold temperatures and wet conditions throughout the spring and summer months of 1996 were likely responsible for the nesting failures detected on Wheeler Mountain and the fewer number of nest sites found than in 1995 and 1994, despite the record number of owls detected in 1996. Low food supply was strongly suspected to contribute significantly to lower nesting numbers than previous years and high rates of nesting failure. Multi-year foraging data for Wheeler Mountain suggests that Flammulated Owls are highly opportunistic and will prey on locally abundant insects, including late larval instar stages of the western spruce budworm during its cyclical outbreak (van Woudenberg 1992). Adult nesting Flammulated Owls were observed gleaning budworm from young Douglas-fir crowns throughout the nesting period in 1990. Photography data indicate that Flammulated Owls may have been using orthopteran species disproportionately in low years of the budworm cycle, 1994-1996 (the western spruce budworm follows a 7-year cycle, Koot *et al.* 1990). The preliminary results suggest that climate may have reduced the availability of supplemental insect prey, reducing overall nesting success. At its northern range limit, the Flammulated Owl may be an opportunistic predator tracking insect cycles by preying on the locally abundant, large-bodied insects. This life strategy could predispose Flammulated Owls to fluctuate in nesting numbers from year to year at their northern range; this characteristic necessitates successive year standardized population inventories.

Poor productivity for Flammulated Owls in 1996 may have been confounded by higher numbers of predators. In the southern interior of B.C., Barred Owls (*Strix varia*) appear to present the greatest predatory risk to Flammulated Owls and this risk is likely greatest at the time of fledging (van Woudenberg 1992). Our observational data for several years (1989-1991, 1994-1996; one survey 1991) suggest that in 1996, Barred Owls may have been more abundant than in previous years. Barred Owls have been observed harassing Flammulated Owls at their nests on several occasions; the results have been Flammulated Owl nest abandonment and strong evidence for fledgling predation. In the Kamloops area, adult Flammulated Owls have always been observed to remain within thickets of young Douglas-fir, where the closely spaced stems inhibit maneuverability of larger birds. These observations suggest adult Flammulated Owls are much less at risk from predation than fledglings.

INVENTORY RECOMMENDATIONS

Relative densities for owls present in an area must be estimated using a standardized census replicated within and between seasons. Census points should be recorded using a hand-held GPS and call bearings should be entered into a GIS for accuracy of bearing triangulation. Triangulated bearings of calls can be used in estimating the numbers of birds in an area. Bearings of owl calls recorded at intervening points between the 500 m census stops may contribute to the precision of using bearing triangulation for bird locations. Density estimates of owls present in an area cannot be used to estimate territorial occupancy due to census bias resulting from (1) the high risk of error associated with estimating distances of calling birds, particularly by inexperienced surveyors; (2) the inability to rule out detecting the same calling male at more than one census stop; and (3) the potential for surplus birds to be recorded en route during migration.

Census surveys must be linked to nesting surveys for standardization. Mapped census data will increase both the efficiency of nest site surveys and accuracy of estimated relative nesting density. Censes must be replicated throughout the time migrants are arriving to help identify potential nest site locations. Areas where few birds are detected only during early arrival time may be highly productive areas. Nest sites should be searched along systematic transects that traverse both the surrounding area of a triangulated bearing location and areas of potential habitat identified from aerial photographs. Nest searches must be conducted at times other than the heat of the day, when adult female owls may roost in nearby trees if the temperature within the nest cavity increases.

The inventory procedure must be selected to meet the information requirements of the management objective for an area. Census data alone should not be extended beyond habitat capability assessment. Nest site surveys in combination with replicated censes are necessary for habitat suitability assessment and to develop management prescriptions. If several owls are detected during censes in an area, but no nests are found, critical features such as cavities in larger trees or snags (> 35 cm d.b.h.), food supply, or security cover may be limiting; the area would be assessed as capable but not suitable nesting habitat.

Recruitment into the population is the most revealing measure of habitat suitability and will identify sink and source habitats. Banding and radio-telemetry of fledglings will provide the greatest accuracy of population trends over multiple years; although less accurate, successive year nesting densities are less costly and may provide trend data to help identify sink and source habitats. Population information can be integrated into landscape management plans; suitable mosaic patterns can be developed to contribute to the sustainability of Flammulated Owl populations at the northern edge of their range.

CONCLUSIONS

There is an increasing trend among resource managers toward standardization of wildlife monitoring. The sustainable management of Flammulated Owls is dependent on the accuracy of the inventory data. Landscape management prescriptions developed for sustainability of breeding Flammulated Owl populations will be effective if sites of habitat capability and suitability are identified.

Accurate habitat inventory is particularly important at the species' northern range where populations may fluctuate from year to year. Changes in predator numbers can contribute to fluctuations in Flammulated Owl populations by reducing recruitment. Differences in annual population numbers necessitate multi-year, comprehensive, standardized census and nest site surveys conducted in combination. Recruitment information will indicate long-term population trends that can be used to identify areas of high productivity (source habitats) for retention in management plans at the northern limits of the species' range.

For those interested in determining the presence or absence of owls, we recommend that a minimum 4-5 visits be conducted to each of the census points. For those engaged in demographic studies of the owls, more visits are needed to detect a greater percentage of the birds; we recommend a minimum of 5-7 visits. Census efforts should be conducted between mid-May to mid-June.

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LITERATURE CITED

Cannings, R.J. 1982. A Flammulated Owl nest in a nest box. The Murrelet. 63(2): 66-68.

Howie, R.R.; Ritcey, R. 1987. Distribution, habitat selection, and densities of Flammulated Owls in British Columbia. In: Nero, R.W.; Clark, R.J.; Knapton, R.J.; Hamre, R.H., eds. Biology and conservation of northern forest owls: symposium proceedings; 1987 February 3-7; Winnipeg, MB. Gen. Tech. Rep. RM-142. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 249-254.

Kamloops Land and Resource Management Planning (LRMP) Team. 1995. Kamloops Land and Resource Management Plan. Province of British Columbia.

Koot, H.P.; Hodge, J. 1990. Forest insect and disease conditions: Kamloops Forest Region 1990. FIDS Rep. 91-2. Forestry Canada.

Lloyd, D.; Angove, K.; Hope, G.; Thompson, C. 1990. A guide to site identification and interpretation for the Kamloops Forest Region. Land Manage. Handb. 23. Victoria, BC: British Columbia Ministry of Forests,

McCallum, D.A. 1994. Review of technical knowledge: Flammulated Owls. In: Hayward, G.D.; Verner, J., tech. eds. Flammulated, Boreal, and Great Gray Owls in the United States: a technical conservation assessment. Gen. Tech. Rep. RM-253. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station.

Mitchell, W.R.; Green, R.E. 1981. Identification and interpretation of ecosystems of the western Kamloops Forest Region. Land Manage. Handb. 2, Vol. 1: Very dry climatic region. Victoria, BC: Ministry of Forests.

Reynolds, R.T.; Linkhart, B.D. 1987a. The nesting biology of Flammulated Owls in Colorado. In: Nero, R.W.; Clark, R.J.; Knapton, R.J.; Hamre, R.H., eds. Biology and conservation of northern forest owls: symposium proceedings; 1987 February 3-7; Winnipeg, MB. Gen. Tech. Rep. RM-142. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 239-248.

Reynolds, R.T.; Linkhart, B.D. 1987b. Fidelity to territory and mate in Flammulated Owls. In: Nero, R.W.; Clark, R.J.; Knapton, R.J.; Hamre, R.H., eds. Biology and conservation of northern forest owls: symposium proceedings; 1987 February 3-7; Winnipeg, MB. Gen. Tech. Rep. RM-142. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 234-238.

van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management. 47(4): 893-901.

van Woudenberg, A.M. 1992. Integrated management of Flammulated Owl breeding habitat and timber harvest in British Columbia. University of B.C. 56 p. Master's thesis.

Watts, S., ed. 1983. Forestry handbook for British Columbia, 4th ed. Forestry Undergraduate Society, UBC. Canada: D.W. Friesen & Sons. Ltd. 611 p.

Habitat Fragmentation and Burrowing Owls (*Speotyto cunicularia*) in Saskatchewan

Robert G. Warnock and Paul C. James[1]

Abstract.—The relationship between landscape (125,664 ha circular plots) fragmentation patterns and the spatial distribution of Burrowing Owls (*Speotyto cunicularia*) was investigated in the heavily fragmented grasslands of Saskatchewan. Data were collected from 152 Burrowing Owl sites and 250 random sites located on 1990 LANDSAT-TM satellite images and 1:250,000 scale topographic maps. Habitat continuity, patch dimensions and isolation of sites were characterized by 15 variables. The stepwise discriminant function analyses showed that owls were not nesting randomly across the landscape. Habitat continuity and patch dimensions were more important than isolation in describing differences between owl and randomly selected sites within the core, but not in the periphery. The preferred soil type for nesting, lacustrine, was more limited in the core range which may also influence the nesting distribution of Burrowing Owls. These results suggest that Burrowing Owls chose the best remaining and not the largest pieces of habitat, near other owl sites.

Worldwide, habitat destruction is considered a major cause of wildlife extinctions (Wilson 1989). Habitat fragmentation is the process by which a large and continuous block of natural habitat is transformed into much smaller and isolated patches by human activity (Noss and Csuti 1994). However, wildlife populations may decline not only when habitats are directly eliminated, but also when natural habitats are fragmented to varying degrees. Habitat fragmentation is an important issue in modern conservation biology because the impacts on wildlife populations can be greater than what is predicted based on the area of the habitat removed alone (Robinson *et al.* 1992).

Due to agriculture, The Great Plains of North America is one of the most heavily modified and fragmented ecosystems in the world (Rowe 1987). These grasslands have variable, sometimes high, plant species diversity because of differences in climatic conditions, topography, soil parent material, and the frequency and intensity of disturbances such as fire (Risser 1988). However, a greater proportion of the avifauna in grasslands has been declining in the last few decades than avifauna in forest habitats (Askins 1993, Herkert 1995, Knopf 1994, Warner 1994). Modern agricultural practices, reduction of grassland habitats into smaller and more isolated patches, removal of native grazers, fire suppression, the expansion of woody vegetation, and recent increases in some predators and brood parasites are often cited as possible causes of these declines (Herkert 1994, Knick and Rotenberry 1995, Knopf 1994, Miller *et al.* 1994, Vickery *et al.* 1994, Warner 1994).

Some raptor species respond quickly to habitat degradation including fragmentation because of their high trophic positions, low densities and large area requirements (Newton 1979). In North America, studies have shown or suggested sensitivity to habitat fragmentation at a local or study site scale in Northern Spotted Owls (*Strix occidentalis caurina*) (e.g., Hunter 1995 *et al.*, Lehmkuhl and Raphael 1993), Flammulated Owls, (*Otus flammeolus*) (Shafer

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1993), Barn Owls (*Tyto alba*) (Colvin 1985), Short-eared Owls (*Asio flammeus*) (Robinson 1991), Northern Harriers (*Circus cyaneus*) (Robinson 1991), Ferruginous Hawks (*Buteo regalis*) (Schmutz 1987) and Swainson's Hawks (*Buteo swainsoni*) (Schmutz 1987), and Burrowing Owls (*Speotyto cunicularia*) (James 1993, Warnock 1996).

The Burrowing Owl uses mammal burrows in well-drained grasslands and agricultural areas from Canada to Argentina and Chile (Haug *et al.* 1993). Because they are often found in farmland, the Burrowing Owl was believed to be more tolerant of cultivation than other raptors (Lepitch 1994). However, the Burrowing Owl population has declined precipitously in Canada from 2,500 pairs to about 1,000 pairs over the last decade (Wellicome and Haug 1995). Due to this trend, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) classified the Burrowing Owl as an endangered species (Wellicome and Haug 1995). A demographic model of Saskatchewan Burrowing Owls predicts extirpation within 20 years (James *et al.*, in press).

The present extent of Burrowing Owl breeding habitat is estimated at only 27 percent of the prairies in Saskatchewan (Wellicome and Haug 1995). It should be noted that this estimate includes land that is not suitable for Burrowing Owls (e.g., rocky soil, hilly terrain, regularly flooded lowland). As a result, cultivation of Burrowing Owl habitat has occurred more quickly (up to 3 percent per year from 1979 to 1986) than the rate of reduction in pasture land suggests (0.8 percent per year between 1966 and 1991) (Hjertaas and Lyon 1987, Wellicome and Haug 1995). Lacustrine soils make ideal habitat for primary burrowers' and support the largest number of Burrowing Owls compared with other soil types (Wellicome and Haug 1995). However, these soils are heavily fragmented because they make choice farmland.

The purpose of this study was to examine the relationships between habitat continuity, patch dimensions, isolation, and the spatial distribution of 152 Burrowing Owl sites in Saskatchewan at a large landscape scale (125,664 ha area). Specifically, we wanted to detect any differences between randomly-selected locations and owl locations in the core and peripheral portions of the owl range, and relate the results to Burrowing Owl ecology and management.

METHODS

Data Collection and Processing

Operation Burrowing Owl (OBO) is a private land stewardship program designed to protect and enhance Burrowing Owl nesting habitat (Dundas 1996). It is the only available data set with many nesting sites from the current Burrowing Owl range in Saskatchewan (about 169,000 km^2). It contains information about the number of nesting pairs since 1987 at each OBO site. We mapped 1,144 owl breeding sites onto 1:250,000 scale topographic maps and found them on 19 1990 LANDSAT-TM satellite images. The satellite images were taken in the fall of 1990. It was assumed that those habitat patterns in 1990 were constant and representative for the whole period. Of course, this was not strictly true as habitat loss and fragmentation continued over this period. In addition, habitats in the satellite images were classified as potential owl breeding habitat (pasture/grassland) and non-owl habitats (all other cover types) based on known Burrowing Owl habitat preferences (Haug *et al.* 1993).

A projector called a Pro-Com 2 (Glengarry GeoScience Ltd., Ottawa) was used to magnify the images to a scale of 1:125,000, and project the images onto a table for the recording of habitat patterns. This scale was selected because it gave the best compromise between magnification and resolution. Scale is important because it influences the questions that can be addressed, procedures followed, the observations obtained, and the interpretation of the results (Andren 1994). At this scale, patch size of 4 ha and a linear distance of 200 m represents the lowest limit of resolution for accurate measurement purposes. The upper limit of resolution was 125,664 ha (20 km radius).

Plot size selection was determined by fine or coarseness of the landscape and the acquisition of statistically adequate sample sizes. To resolve these issues, the foraging plot size of 2.7 km radius (2,290 ha area) and the dispersal plot size of 20 km radius (125,664 ha area) were used in this study. The foraging plot size was based on the maximum foraging distance of Burrowing Owls in Saskatchewan

(Haug and Oliphant 1990). The dispersal plot size was based on our unpublished median year to year breeding dispersal distance of owls in Saskatchewan (James, unpubl. data).

We selected 117 OBO sites with 7 years (1987-1993) of complete data plus an additional 35 OBO sites with 6 years of data, to maximize sample sizes. If the plots of individual owl sites did overlap 50 or more percent at the 20 km radius, only one site was selected. The selection was based on the site with the maximum number of years of verified owl data. If they were the same, one site was randomly selected. This was done in an attempt to control for statistical independence of random and owl locations. Two hundred and fifty random sites of any habitat, not occupied by owls, were also selected from the satellite image and located on the 1:250,000 scale topographic maps.

An arbitrary minimum owl site density was used to classify random and OBO (owl) sites as either core or peripheral. Areas with a minimum OBO site density of 1.5 per 1,000 km² or greater were classified as core. The OBO density of 1.5 sites per 1,000 km² is equivalent to six OBO sites per quadrat (about 4,000 km²) in figure 1. The peripheral portion of the owl range was defined by an OBO site density of less than 1.5 sites per 1,000 km² (fig. 1).

All habitat patterns and all OBO sites within a 20 km radius of the 152 selected OBO sites and the 250 random locations were recorded onto white sheets ("habitat sheets") at the selected scale of 1:125,000. A planimeter was used to measure areas of natural habitat patches. A digital measuring wheel was used to measure edges of natural habitat patches and distances between natural habitat patches. The shortest edge to edge distances were measured between habitat patches. Distances between owl sites were measured on the 1:250,000 scale topographic maps.

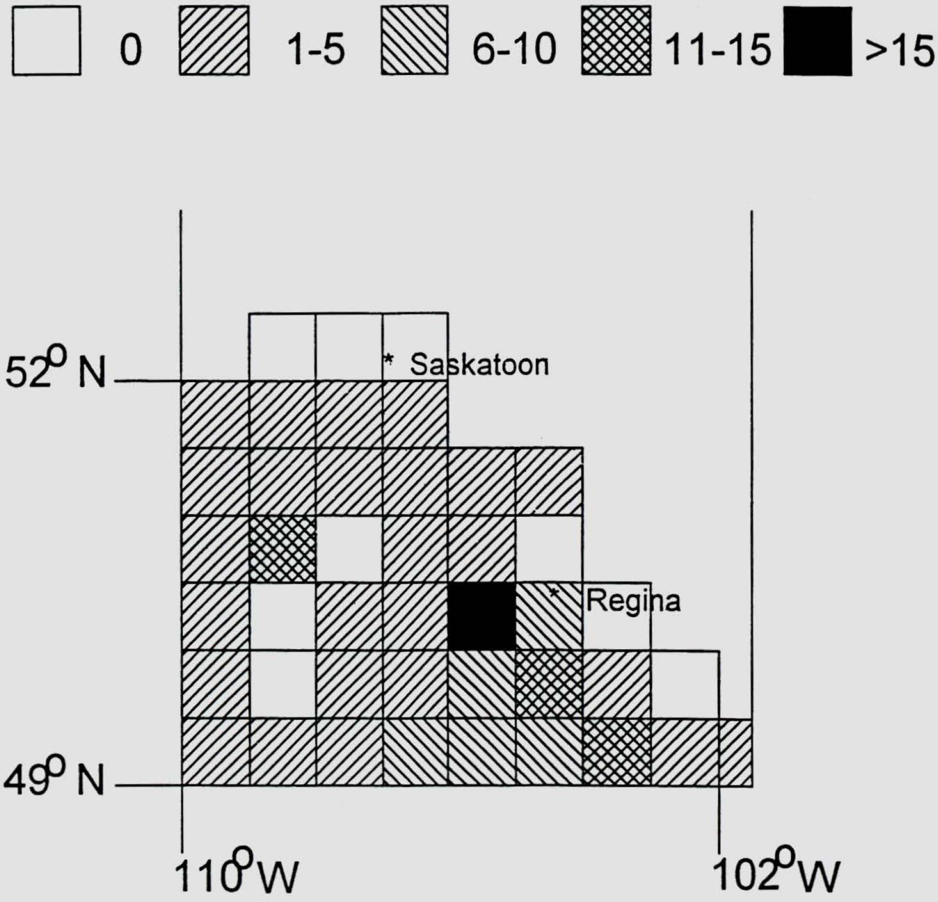

Figure 1.—*Numbers and distribution of occupied sites or "colonies" as reported by Operation Burrowing Owl in Saskatchewan in 1993. Each square represents a quarter of a 1:250,000 scale map sheet. The core portion of the Saskatchewan Burrowing Owl (*Speotyto cunicularia*) range was delineated by squares with six or more sites in 1993 (modified from Wellicome and Haug 1995).*

Previous work has shown that continuity, patch dimensions and isolation of natural habitat patches can have important effects on animal populations (see Herkert 1994, Knick and Rotenberry 1995, Vickery *et al.* 1994). Continuity of habitats within the two plot sizes (2,290 and 125,664 ha) for each owl and random site was measured with four variables: percent grassland (%G 20), total area to total edge ratio (A/E), number of patches (No.P.), and percent grassland to number of patches ratio (%G/No.P) (table 1). Area (AOP), perimeter or edge (EOP), and shape (AOP/EOP) of patches were measured for patches containing either a selected owl or a random site (table 1). Three common isolation measures were used in this study: distance to the nearest patch (DNP), distance to the second nearest patch (DNNP), and distance to the nearest owl site (DNO) (table 1). The number of owl sites (No. Sites) were counted within a 20 km radius of an owl or random site (table 1). The number of sites is another indicator of isolation because the number of nearby known sites should decline with increased habitat fragmentation.

Statistical Analyses

This study was correlative in nature; thus cause and effect were inferred rather than experimentally demonstrated unlike Diffendorfer *et al.* (1995) and Robinson *et al.* (1992). Four assumptions for parametric univariate and multivariate analyses were examined: randomness and independence of sites, the normality of variables (Shapiro-Wilks' W test), and the equality of variances (Levene's test). Data were log or square root transformed to normalize the data where possible (table 1). Unless indicated, all statistical procedures were run with Statistica for Windows (StatSoft Inc. 1994).

Previous work showed that core and peripheral portions of the owl range were significantly different in patterns of habitat fragmentation (Warnock 1996). Tukey's Honest Significant Difference (HSD) (a variant of ANOVA) test for unequal sample sizes was used for normalized variables. The nonparametric Mann-Whitney U-test was used for variables that could not be normalized through transformations (Sokal and Rohlf 1981). These univariate tests were used to compare owl sites and random sites. Multivariate stepwise discriminant function analysis (DFA) is commonly used to assess the effectiveness of variable sets in discriminating between groups. Two DFAs were used to find out which measured components were most correlated with the discrimination of owl and random

Table 1.—*Abbreviations and units of variables used in Saskatchewan Burrowing Owl (*Speotyto cunicularia*) study.*

Variable	Description
%G	Percent grassland. (log transformed at 20 km radius and non-transformed at 2.7 km radius.)
A/E	Total area to total edge ratio in ha/km. (log transformed at 20 km radius and non-transformed at 2.7 km radius).
No.P.	Number of patches. (log transformed at 20 km radius and non-transformed at 2.7 km radius).
%G/No.P	Percent grassland to number of patches ratio. (log transformed at 20 km radius and non-transformed at 2.7 km radius).
AOP	Area of patch containing either an owl or random location in ha. (Non-transformed).
EOP	Total edge of patch containing either an owl or random location in ha. (Non-transformed).
AOP/EOP	Area to edge ratio for owl or random patch in ha/km. (Non-transformed).
DNP	Distance to the nearest patch in km. (Square-root transformed).
DNNP	Distance to the second nearest patch in km. (Square-root transformed).
DNO	Distance to the nearest owl location in km. (Log transformed).
No. Sites	Number or nearby owl sites within 20 km radius. (Non-transformed).
N	Sample Size

A 20 km radius is based on the median breeding dispersal of owls and a 2.7 km radius is based on the maximum foraging distance of owls. Untransformable refers to an inability to obtain a normal distribution of data or a skewed distribution due to small sample sizes. Logarithmic (log) and square-root transformations were used to normalize variables where possible for analyses.

locations in the core and peripheral owl ranges in Saskatchewan. A chance corrected classification was used to remove the effects of chance on statistical significance of each DFA (Titus *et al.* 1984).

RESULTS AND DISCUSSION

Peripheral owl sites had much greater ($P < 0.05$) continuity of natural habitat within a 20 km radius (%G) than peripheral random locations (table 2). This result is consistent with the habitat fragmentation hypothesis. With this hypothesis, one can predict more habitat around nest sites of habitat fragmentation sensitive species than random locations. For example, similar results were obtained in several habitat patterns studies of the Northern Spotted Owl, a habitat fragmentation sensitive species (e.g., Hunter *et al.* 1995, Lehmkuhl and Raphael 1993).

In the core owl range, owl locations had much lower continuity of habitat ($P < 0.05$) within a 20 km radius with smaller A/E and %G/No.P ratios and larger number of patches (table 2). Patch dimensions of core owl locations were much smaller ($P < 0.05$) than random locations (AOP and AOP/EOP) (table 2). These results support the reported field observations of Saskatchewan Burrowing Owls nesting in small habitat patches (Haug, 1985, Houston *et al.* 1996). Similar results were shown for the Great Horned Owl *(Bubo virginianus)* (Hunter *et al.* 1995). If one accepts the habitat fragmentation hypothesis, larger numbers of a 'sensitive' species should be in contiguous and less isolated patches (e.g., Hanski 1994). A variety of factors could explain the distribution of core owl locations. They include habitat quality effects on habitat selection (see below) and bias in having Operation Burrowing Owl sites in a very fragmented natural landscape in the core Burrowing Owl range in Saskatchewan.

It appeared that owls prefer more fragmented but less isolated habitat in the core (table 2). This preference may be due to habitat selection at a lower scale where burrow and prey availability (related to soil type), are the primary determinants. Abundance of Burrowing Owls is probably greatest with lacustrine soils, because of higher burrow availability (Wellicome and Haug 1995). Soil types appeared to be a factor in Burrowing Owl abundance and distribution by determining the presence of ground squirrels, voles, and deer mice (Laundre and Reynolds 1993). Also, previous work showed that proportions of the major soil types did differ significantly between the core

Table 2.—*Significant differences between Burrowing Owl (*Speotyto cunicularia*) and random sites in the core and peripheral ranges in Saskatchewan (P < 0.05).*

	Core range			Peripheral range	
Variable	**Owl**	**Random**	**Variable**	**Owl**	**Random**
N	57	53	N	95	197
A/E20*	56.27 ± 3.49	73.19 ± 5.26	%G20*	19.20 ± 1.33	16.19 ± 1.23
No.P20*	52.05 ± 1.98	38.24 ± 1.64	DNO*	5.75 ± 0.52	23.10 ± 1.93
%G/NoP20*	0.34 ± 0.04	0.61 ± 0.08	No.Sites#	6.02 ± 0.41	3.21 ± 0.26
No.P2.7#	2.49 ± 0.18	1.74 ± 0.13			
AOP#	2403 ± 790	8022 ± 3079			
AOP/EOP#	27.52 ± 5.87	43.21 ± 8.53			
DNP*	1.21 ± 0.12	1.88 ± 0.17			
DNNP*	2.01 ± 0.16	2.65 ± 0.12			
DNO	3.83 ± 0.57	5.31 ± 0.55			

Reported means of landscape characteristics (± 1 SE). are untransformed.

* = Tukey's Honest Significant Difference for unequal sample sizes (ANOVA).

= Mann-Whitney U-test.

20 = 20 km radius. 2.7 = 2.7 km radius.

and the periphery ($P < 0.05$). Specifically, the core had significantly less of the primary burrowers' (ground squirrels) preferred lacustrine soil type (22.7 percent of landscape) than the peripheral range (33.7 percent of landscape) (Warnock 1996). Lacustrine soils make ideal burrow substrates and farmland because they are flat, have few rocks and are sandy or silty loam soils (Wellicome and Haug 1995). These results suggest that optimal Burrowing Owl habitat is more limiting and that owls could be selecting the best remaining not the largest blocks of habitat in the core range. In other words, more Burrowing Owls have been found in small uncultivated patches with lacustrine soils than any other cover type.

However, nesting in small natural patches may have additional risks. For example, Haug (1985) found that Burrowing Owl home range size increased with the percentage of cultivation. In fragmented landscapes, Burrowing Owls may forage greater distances and spend more time away from the nest, making them more vulnerable to predators, and therefore, less efficient at reproduction. Some highly fragmented owl locations used in this study had very many pairs from 1987 to 1993. Higher raptor densities in small habitat fragments have been reported before in the literature (e.g., James 1993, Loman 1991). Crowding into small patches can increase foraging interference, aggression, and conspecific predation (Saunders *et al.* 1991). Intraspecific competition is thought to be a major cause of nest abandonment and low productivity of dense Burrowing Owl colonies (Green and Anthony 1989). High densities of nests may attract predators while lower densities would force the predators to concentrate on their staple prey (Sugden and Beyersbergen 1986). Stochastic events such as flooding and predation are also likely to increase the probability of nest site abandonment by Burrowing Owls from small habitat fragments (Hinsley *et al.* 1995). These events may explain the population decline of the Burrowing Owl in Saskatchewan (Warnock 1996).

In highly fragmented areas, such as the core of the range, edges becomes important. Edge habitats predominate in fragmented landscapes. Many studies have shown that artificial nests (e.g., Burger *et al.* 1994) and natural nests (Johnson and Temple 1990) suffer greater predation rates when placed near edges. Owls nesting near edges would suffer greater predation because predators have been shown to search more thoroughly along pasture edges near cover (Sugden and Beyersbergen 1986). Nest predation is a major cause of nest failure and abandonment in Burrowing Owls (Green and Anthony 1989, Wellicome and Haug 1995). Burrowing Owls do not avoid pasture edges because their breeding season does start before crop seeding begins, when visibility is still good near cultivated fields, thus they may be adversely affected by edge effects (Wellicome and Haug 1995).

Peripheral owl sites were near more owl sites (No.Sites) than random locations in the periphery (table 2). Isolation was much lower ($P < 0.05$) for owl sites than for random locations in the core (DNP, DNNP, and DNO) and peripheral portions of the range (DNO) in Saskatchewan (table 2). Isolation may be less important in the core because the fragments although smaller are closer together and owl site density (although declining, Warnock 1996) was greater than in the periphery. Nesting near other owls in the periphery may be important for successful dispersal and pairing success (Faaborg *et al.* 1993). A reduced amount of isolation was also important for the presence of several tall-grass prairie birds (Sampson 1980), and Columbian ground squirrels (*Spermophilus columbians* (Ordi)) (Weddell 1991) in natural habitat patches.

Two stepwise DFAs (table 3) correctly classified more owl and random sites than predicted by chance alone in the core and periphery ($P < 0.05$) (Titus *et al.* 1984). The following variables (and their correlation coefficients) were important in distinguishing core owl locations and core random locations: the number of patches in a 20 km radius (0.743), isolation (DNNP (0.739), DNO (0.663)), and patch dimensions (AOP/EOP (0.648)). In the periphery, the following variables (and their correlation coefficients) were important in distinguishing owl locations from random locations: isolation (DNO (0.888)), number of patches in a 2.7 km radius (0.727), continuity of habitat (%G/No.P (2.7) (0.744), (A/E (20) (0.733)), and the patch area (AOP, (O.723)). These results suggest that Burrowing Owls were not nesting randomly across the landscape (tables 2 and 3). These results are supported by Duncan (1995) who mapped known owl sites in the last 7 to 14 years on the Canadian prairies. For example, there were well-defined concentrations of Burrowing Owl sites and large tracts in the

Table 3.—*Stepwise discriminant function analyses of core and peripheral Burrowing Owl (*Speotyto cunicularia*) sites in Saskatchewan.*

Core sites		Peripheral sites	
Group	**Correctly classified**	**Group**	**Correctly classified**
Owl (N = 57)	78.95%	Owl (N = 110)	47.74%
Random (N = 95)	77.36%	Random (N = 197)	91.33%
Total (N = 110)	78.18%	Total (N = 292)	76.71%
Z=	5.57	Z=	5.90
P=	0.0001	*P*=	0.0001

peripheral area that seemed lacking owls. It is likely that the spatial arrangement (tables 2 and 3) and the habitat quality of patches and historical and stochastic processes likely influence owl distribution, once the locational bias in the OBO database is removed (Hinsley *et al.* 1995).

Owl sites may be more limited in the periphery than in the core because most owl sites were 'misclassified' a posteriori by the DFA model as random sites (table 3). Habitat modification at distant sites could affect the distribution of existing Burrowing Owl sites by increasing the distance between sites and thus decreasing the probability of dispersal between owl sites. Isolation interrupts the flow of individuals between patches and lowers the probability of individuals dispersing from or into them (Fahrig and Merriam 1994). Burrowing Owls can travel the distances between patches and owl sites. However, isolation increases predation exposure, increases delays in finding another owl colony, nest burrow, or mate, and lowers the feeding efficiency. This may help to explain nesting in sub-optimal habitats such as roadsides, cropland or fallow (Wellicome and Haug 1995). In short, isolation may determine how much risk associated with dispersal, and thus the year-to-year occupancy of owl sites (Faaborg *et al.* 1993).

CONSERVATION IMPLICATIONS

Burrowing Owls have the capacity for rapid population recovery because of their high reproductive potential and their broad prey spectrum (Wellicome and Haug 1995). We recommend that management focus on the core portion of the Burrowing Owl range in Saskatchewan because the core contains most of the remaining owls and the population decline there is less severe (Warnock 1996). Stabilizing the core population will be critical for the long-term conservation of the species in Saskatchewan. The core will likely serve as a 'source' where reproductive output is greater than mortality. Such sources have maintained regional populations of Midwestern forest songbirds (Robinson *et al.* 1995). The results of this study suggest that maximizing the continuity of habitat and increasing the number of accessible patches with optimal dimensions in the core range would be a good strategy.

The conservation of the Burrowing Owl has a high level of support in Saskatchewan and many habitat patches are already protected under Operation Burrowing Owl (Wellicome and Haug 1995). However, additional patches in private and public ownership could be protected. Most of the known Burrowing Owl sites are on private land (an artifact of OBO). The provincial and federal governments hold title to most of the remaining large prairie blocks in Saskatchewan but the distribution of Burrowing Owls on these lands is poorly known (Wellicome and Haug 1995). To increase the continuity of Burrowing Owl habitat, additional private and public Burrowing Owl habitat needs to be identified and protected through close coordination and cooperation between conservation agencies and private landowners and Crown land leasees.

If the core population is stabilized, the focus could then shift to persistent peripheral owl sites. Occupancy can be enhanced by increasing habitat quality, lowering isolation between nearby owl sites and the source population, minimization of fragmentation in the maximum foraging distance and minimization of patch edges of persistent owl sites. We would hope that these would become mini-sources within the periphery.

In conclusion, it appeared that patterns of habitat fragmentation affected the abundance and distribution of owl sites. Therefore, it is likely that habitat fragmentation on the breeding grounds has been a major contributing factor in the decline of Burrowing Owl in Saskatchewan. However, remember that the study was correlative in nature, and thus cause and effect relationships were inferred rather than proved. Demographic parameters for Burrowing Owls are only now being quantified and the understanding of the relationship between habitat fragmentation and demographic processes require more work (James *et al.* 1997). The conservation of the Burrowing Owl and the prairie ecosystem are intertwined. We can reduce the impacts of habitat fragmentation on Burrowing Owls and costs of their recovery by creating and protecting additional grassland habitat.

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LITERATURE CITED

Andren, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos. 71: 355-366.

Askins, R.A. 1993. Population trends in grassland, shrubland and forest birds in eastern North America. Current Ornithology. 11: 1-34.

Burger, L.D.; Burger, L.W., Jr.; Faaborg, J. 1994. Effects of prairie fragmentation on predation on artificial nests. Journal of Wildlife Management. 58: 249-254.

Colvin, B.A. 1985. Common Barn Owl population decline in Ohio and the relationship to agricultural practices. Journal of Field Ornithology. 56: 224-235.

Diffendorfer, J.E.; Gaine, M.S.; Holt, R.D. 1995. Habitat fragmentation and movements of three small mammals (*Sigmodon, Microtus* and *Peromyscus*). Ecology. 76: 827-839.

Duncan, J.R. 1995. Burrowing Owl nesting distribution map for the prairie provinces. Winnipeg, MB: Manitoba Department of Natural Resources.

Dundas, H. 1996. 1995 Saskatchewan Operation Burrowing Owl annual report. Regina, SK: Nature Saskatchewan.

Faaborg, J.; Brittingham, M.; Donovan, T.; Blake, J. 1993. Habitat fragmentation in the temperate zone: a perspective for managers. In: Finch, D.M.; Stangel, P.W., eds. Status and management of Neotropical migratory birds; 1992 September 21-25; Estes Park, CO. Gen. Tech. Rep. RM-229. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 331-338.

Fahrig, L.; Merriam, G. 1994. Conservation of fragmented populations. Conservation Biology. 8: 50-59.

Green, G.A.; Anthony, R.G. 1989. Nesting success and habitat relationships of Burrowing Owls in the Columbia Basin. Condor. 91: 347-351.

Hanski, I.K. 1994. Patch occupancy dynamics in fragmented landscapes. Trends in Ecology and Evolution. 9: 131-135.

Haug, E.A. 1985. Observations on the breeding ecology of Burrowing Owls in Saskatchewan. Saskatoon, SK: University of Saskatchewan. M.S. thesis.

Haug, E.A.; Millsap, B.A.; Marte, M.S.,II. 1993. Burrowing Owl (*Speotyto cunicularia*). In: Poole, A.; Gill, F., eds. The birds of North America. No. 61. Philadelphia, PA: The Academy of Sciences; Washington, DC: The American Ornithologists Union.

Haug, E.A.; Oliphant, L.W. 1990. Movements, activity patterns, and habitat use of Burrowing Owls in Saskatchewan. Journal of Wildlife Management. 54: 27-35.

Herkert, J.R. 1994. The effects of habitat fragmentation on midwestern grassland communities. Ecological Applications. 4: 461-474.

Herkert, J.R. 1995. Analysis of midwestern breeding bird population trends: 1966-1993. American Midland Naturalist. 134: 41-50.

Hinsley, S.A.; Bellamy, P.E.; Newton, I. 1995. Bird species turnover and stochastic extinction in woodland fragments. Ecography. 18: 41-50.

Hjertaas, D.; Lyon, W. 1987. A stratified random survey for Burrowing Owls. Saskatchewan Wildlife Branch Tech. Rep. 87-2. Regina, SK: Saskatchewan Parks and Renewable Resources.

Houston, C.S.; Hjertaas, D.G.; Scott, R.L.; James, P.C. 1996. Experience with Burrowing Owl nest-boxes in Saskatchewan with comment on decreasing range. Blue Jay. 54: 136-140.

Hunter, J.E.; Gutiérrez, R.J.; Franklin, A.B. 1995. Habitat configuration around Spotted Owl sites in northwestern California. Condor. 97: 684-693.

James, P.C. 1993. Habitat fragmentation and Burrowing Owls in Saskatchewan. In: Holroyd, G.L.; Dickson, H.L.; Regnier, M.; Smith, H.C., eds. Proceedings of the 3d prairie conservation and endangered species workshop; 1992 February; Brandon University, Brandon, MB. Natl. Hist. Occas. Pap. 19. Edmonton, AB: Provincial Museum of Alberta: 193-194.

James, P.C.; Ethier, T.J.; Toutloff, M.K. 1997. Parameters of a declining Burrowing Owl population in Saskatchewan. Journal of Raptor Research Report. 9: 34-37.

Johnson, R.G.; Temple, S.A. 1990. Nest predation and brood parasitism of tallgrass prairie birds. Journal of Wildlife Management. 54: 106-111.

Knick, S.T.; Rotenberry, J.T. 1995. Landscape characteristics of fragmented shrub-steppe habitats and breeding passerine birds. Conservation Biology. 9: 1059-1071.

Knopf, F.L. 1994. Avian assemblages on altered grasslands. Studies in Avian Biology. 15: 247-257.

Laundre, J.W.; Reynolds, T.D. 1993. Effects of soil structure on burrow characteristics of five small mammal species. Great Basin Naturalist. 53: 358-366.

Lehmkuhl, J.F.; Raphael, M.G. 1993. Habitat pattern around Northern Spotted Owl locations on the Olympic Peninsula, Washington. Journal of Wildlife Management. 57: 302-315.

Lepitch, D.J. 1994. Agricultural development and its influence on raptors in southern Idaho. Northwest Science. 68: 167-171.

Loman, J. 1991. Small mammal and raptor densities in habitat islands: area effects in a south Swedish agricultural landscape. Landscape Ecology. 5: 183-189.

Miller, B.; Ceballos, G.; Reading, R. 1994. The prairie dog and biotic diversity. Conservation Biology. 8: 677-681.

Newton, I. 1979. Population ecology of raptors. Vermillion, SD: Buteo Books.

Noss, R.F.; Csuti, B. 1994. Habitat fragmentation. In: Meffe, G.K.; Caroll, C.R., eds. Principles of conservation biology. Sunderland, MA: Sinauer Associates: 237-264.

Risser, P.G. 1988. Diversity in and among grasslands. In: Wilson, E.O.; Peter, F.M., eds. Biodiversity. Washington, DC: National Academy Press: 176-180.

Robinson, G.R.; Holt, R.D.; Gaines, M.S.; Hamburg, S.P.; Johnson, M.L.; Fitch, H.S.; Martinko, E.A. 1992. Diverse and contrasting effects of habitat fragmentation. Science. 257: 524-526.

Robinson, S.K. 1991. Effects of habitat fragmentation on midwestern raptors. In: Pendleton, B.G.; Krahe, D.L., eds. The midwest raptor management symposium and workshop. Sci. Tech. Ser. 15. Washington DC: National Wildlife Federation: 195-202.

Robinson, S.K.; Thompson, F.R., III; Donovan, T.M.; Whitehead, D.R.; Faaborg, J. 1995. Regional forest fragmentation and the nesting success of migratory birds. Science. 267: 1987-1990.

Rowe, J.S. 1987. One hundred years of land use. Blue Jay. 45: 127-139.

Sampson, F.B. 1980. Island biogeography and the conservation of prairie birds. In: Kucera, C.L., ed. Proceedings of the 7th North American prairie conference; 1980 August 4-6; Springfield, MO: Southwest Missouri State University: 293-299.

Saunders, D.A.; Hobbs, R.J.; Margules, C.R. 1991. Biological consequences of ecosystem fragmentation: a review. Conservation Biology. 5: 18-32.

Schmutz, J.K. 1987. The effects of agriculture on Ferruginous and Swainson's hawks. Journal of Range Management. 40: 438-440.

Shafer, A-L. 1993. Effects of landscape composition and fragmentation on owl species distribution of the Dixie National Forest. Utah. Logan, UT: Utah State University. M.S. thesis.

Sokal, R.; Rohf, F.J. 1981. Biometry. 2d ed. New York, NY: W.H. Freeman and Company.

StatSoft Inc. 1994. Statistica for windows. Tulsa, OK: StatSoft Inc.

Sugden, G.L.; Beyersbergen, G.W. 1986. Effect of density and concealment on American Crow predation of simulated nests. Journal of Wildlife Management. 50: 9-14.

Titus, K.; Mosher, J.A.; Williams, B.K. 1984. Chance corrected classification for use in discriminant analysis: ecological applications. American Midland Naturalist. 111: 1-7.

Vickery, P.D; Hunter, M.L., Jr.; Melvin, S.M. 1994. Effects of habitat area on the distribution of grassland birds in Maine. Conservation Biology. 8: 1087-1097.

Warner, R.E. 1994. Agricultural land use and grassland habitat in Illinois: future shock for midwestern birds? Conservation Biology. 8: 147-156.

Warnock, R.G. 1996. Spatial, temporal and turnover dynamics of Burrowing Owl (*Speotyto cunicularia*) distribution in the extensively fragmented grasslands of Saskatchewan. Regina, SK: University of Regina. M.S. thesis.

Weddell, B.J. 1991. Distribution and movements of Columbian ground squirrels (*Spermophilus columbians* (Ordi)): are habitat patches like islands? Journal of Biogeography. 18: 385-394.

Wellicome, T.I.; Haug, E.A. 1995. Updated report on the status of the Burrowing Owl (*Speotyto cunicularia*) in Canada.Ottawa, ON: Committee on the Status of Endangered Wildlife in Canada.

Wilson, E.O. 1989. Threats to biodiversity. Scientific American. 261(3): 108-116.

The Effects of Predator Exclusion and Food Supplementation on Burrowing Owl (*Speotyto cunicularia*) Population Change in Saskatchewan

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Abstract.—If low reproductive output plays an important role in the population decline of the Burrowing Owl (*Speotyto cunicularia*) in Canada, we predicted the decline would slow or stop in our study population after consecutive years of productivity enhancement via food supplementation and predator exclusion. In the portion of our study site for which historical data existed, the yearly rate of decline averaged 24.7 percent per year before, and 11.8 percent per year after, productivity enhancement. Our overall study population showed no decline after the first year of treatment, but declined 17 percent following the second year of treatment. Females (both adults and juveniles) showed lower site fidelity and dispersed farther than did males, and juveniles showed lower site fidelity and dispersed farther than did adults. Although adult dispersal distances were small, natal dispersal distances suggest that emigration probably occurs from our study area, increasing the difficulty of detecting a population effect from our treatment.

The Burrowing Owl (*Speotyto cunicularia*) is designated as an Endangered species in Canada because of its severe and ongoing population decline (Hjertaas *et al.* 1995, Wellicome 1997a, Wellicome and Haug 1995). Habitat modification, resulting from the steady increase in intensity of agricultural land-use, is the factor reported to be ultimately responsible for this decline (Haug and Oliphant 1990, Hjertaas *et al.* 1995, Schmutz *et al.* 1991, Wedgwood 1978, Zarn 1974), but proximate factors have yet to be identified (Haug 1985, James and Fox 1987, Wedgwood 1978).

Proximate factors can cause population declines by reducing either recruitment (the number of first-time breeders) or survival of adults, or both (Temple 1986). Canada's Burrowing Owls spend their winters in unknown areas at least as far south as Texas or Mexico (James 1992), and their degree of philopatry to breeding areas has not been measured adequately; hence, it is not yet possible to calculate accurate annual survival rates for adult owls. On the other hand, one important component of recruitment—reproductive output—is determined entirely within the breeding grounds, and has been quantified for several years on two study sites in Canada. The number of young fledged per successful nest has declined significantly over the last decade near both Hanna, Alberta (J.K. Schmutz, unpubl. data), and Regina, Saskatchewan, as has the number of fledglings per nesting attempt in Saskatchewan—the only area for which those data exist (James *et al.* 1997). However, a causal relationship between the observed decline in reproductive output and the decline in population size has not been established.

Predation and food shortage are factors that often limit reproduction in birds and other animals (Martin 1992, McNamara and Houston 1987). Because Burrowing Owls are small ground-nesters, they have many predators: badgers (*Taxidea taxus*), foxes (*Vulpes* spp.), striped skunks (*Mephitus mephitus*), weasels (*Mustela nivalis* and *M. frenata*), and raccoons

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(*Procycon lotor*) enter or excavate burrows and eat eggs, nestlings, and/or adult females (Wellicome and Haug 1995). On the Regina Plain, mammalian predation causes a high nest-failure rate in Burrowing Owls (P.C. James, unpubl. data), and predator exclusion has been suggested as a method to potentially increase nesting success.

Reproductive food-limitation appears to be widespread in Burrowing Owls. In Oklahoma, availability of vertebrate prey in spring was thought to limit the reproductive output of owls (Butts 1973). In Idaho, brood size increased with proximity to irrigated agricultural areas, and prey availability was again suggested as the causal factor (Gleason 1978). Preliminary results from food supplementation experiments on the Regina Plain showed that food intake during brood-rearing limited the number of fledglings produced at successful Burrowing Owl nests (Wellicome 1997b).

If low reproductive output plays an important role in the Burrowing Owl population decline, relative to potential non-breeding effects (e.g., high winter mortality), we predict the decline will slow or stop if owl productivity is successfully increased for several consecutive years in a discrete area. However, the likelihood of detecting such an effect would depend partly on the propensity of individuals to disperse and, thus, sometimes emigrate from the study area. If site fidelity were high and/or dispersal distances small, a positive population response to increased productivity would lead to a higher number of pairs within the study area. However, if site fidelity were low and dispersal distances large, a positive population response would likely not be detected inside the study area because the increased number of recruits would be spread over a wide geographic area.

Here, we present preliminary results from the first 3 years of a 5-year study. Our specific objectives were four-fold:

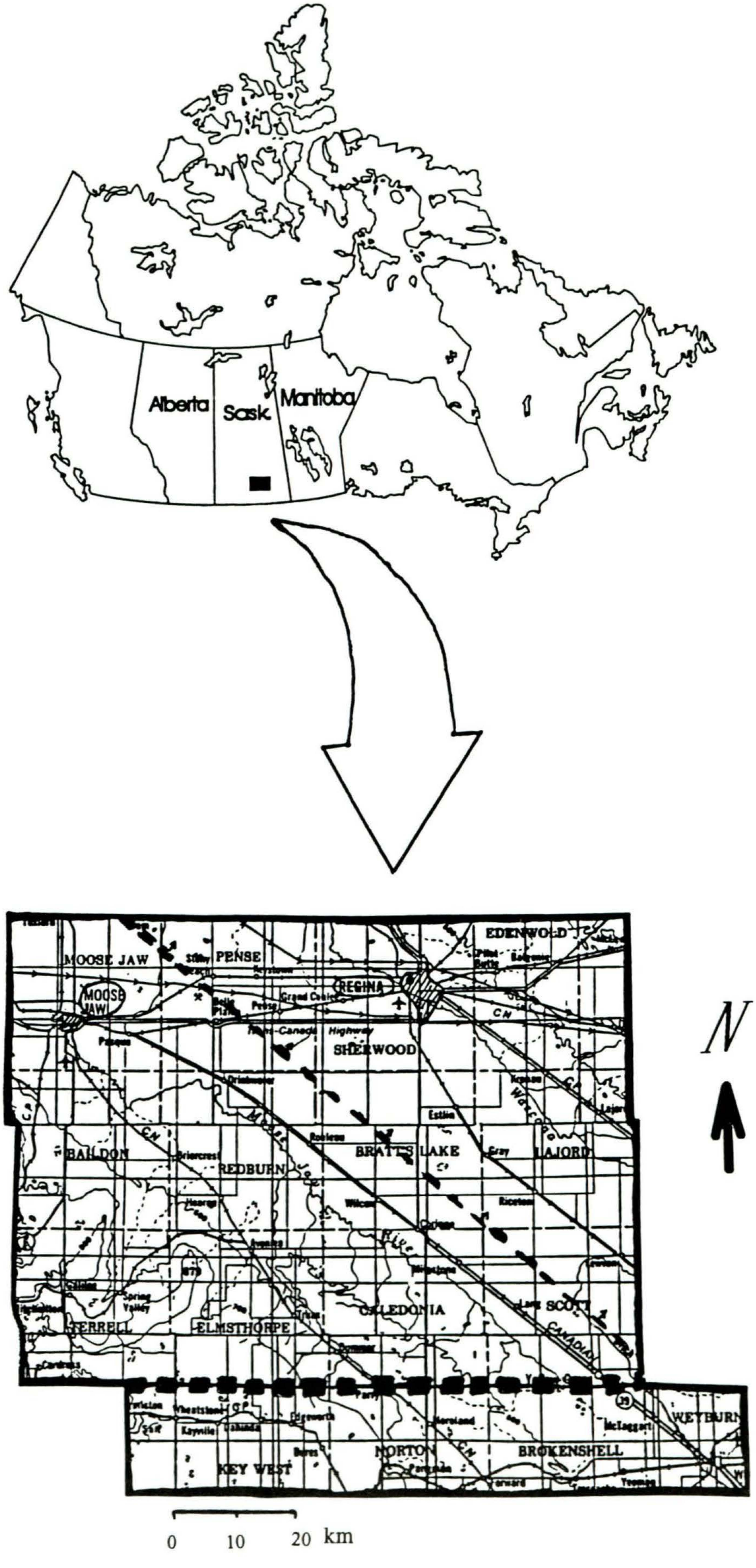
1. To develop and test "predator-proof" artificial nest burrows for increasing the proportion of Burrowing Owl nests that successfully raise young to fledging age.
2. To further assess the effectiveness of supplemental feeding during the nestling stage for increasing the number of young fledged from successful nests.
3. To measure nest-site fidelity and dispersal of adults and juveniles.
4. To determine if increasing the number of fledglings produced per nesting attempt in consecutive years affects the population decline.

METHODS

Burrowing Owls were studied in the Grassland Ecoregion of Saskatchewan (Harris *et al.* 1983) from mid-April to mid-August, 1994-1996, on a 10,000 km^2 site situated south of the cities of Moose Jaw and Regina (108 townships; one township = 9.6 x 9.6 km). The site included the area in which James *et al.* (1997) studied Burrowing Owls between 1987 and 1993 (fig. 1). Thus, data from our experiments can be compared to historical data from the same site. The majority of our study area lies on the Regina Plain, with the southwestern-most portion extending into the Missouri Coteau. In 1996, the study area was expanded southward to encompass an additional 2,200 km^2. Intensive cultivation in this region has left a heavily-fragmented landscape (James *et al.* 1990). Consequently, most owls nest in small, intensively-grazed pastures that are interspersed among a variety of habitat types, including cereal crops, summer fallow, hayland, and other grassland.

Each year within our study area, we visited all sites known to have had owls at least once in the past 5 years, as well as any newly-discovered sites. We searched pastures by driving or walking transects spaced at approximately 25 m, thus passing within 12.5 m of any potential owl burrows. All ground squirrel or badger burrows were scanned for signs of Burrowing Owl activity (whitewash or pellets). In addition, we chose randomly 5 of the 28 townships that were known to have contained at least one pair of owls in 1995, and searched *all* grassland fragments and roadside-ditches within this subset of townships in 1996. We found no additional Burrowing Owl nests with this intensive search method, suggesting that the method of visiting only known sites, or those sites reported to us, missed few (if any) occupied owl nests.

In May, 1 to 2 weeks after each pair had chosen a burrow and begun lining its entrance with nesting material, we installed a wooden artificial nest burrow (fig. 2) in place of the natural burrow. From ground-level, artificial nest burrows (ANBs) looked the same as natural burrows, and we lined the tunnels and nest


Alberta
Sask.
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EDENWOLD
MOOSE JAW
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REGINA
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Grand Coulee
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Trans-Canada Highway
SHERWOOD
Drinkwater
Estlin
Rouleau
BAILDON
Briercrest
REDBURN
BRATT'S LAKE
Gray
LAJORD
Wilcox
Riceton
Corinne
Avonlea
Milestone
Spring Valley
CALEDONIA
LAKE SCOTT
TERRELL
ELMSTHORPE
CANADIAN
Wheatstone
Kayville
Edgeworth
Parry
WEYBURN
McTaggart
NORTON
BROKENSHELL
KEY WEST
Forward
Yeoman
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0
10
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Figure 1.—*Study area on the Regina Plain, Saskatchewan. The extension of the study area in 1996 is shown below the thick dashed line. Historical data were collected by Dr. Paul C. James in the northeastern portion of the study area, indicated with a thin dashed line.*

chambers with dirt and shredded, dry manure to resemble the inside of natural burrows. Nest boxes were introduced before egg-laying, and owls initiated their clutches in the artificial chambers a few days to a few weeks later. Eggs were checked approximately 1 month after laying to establish hatching dates. ANBs were designed to be 'predator proof' from above (fig. 2); i.e., able to exclude fossorial (digging) predators. However, mid-way through the 1994 breeding season, we discovered that one predator—the badger—was able to access nests by digging around and then underneath the bottomless boxes. In 1995 and 1996, we covered the bottoms of most ANBs with metal grates, thus excluding badgers while still maintaining adequate drainage. Many ANBs were occupied in years subsequent to their installation, but when owls chose natural burrows, an effort was made to install predator-proof ANBs. Twenty-four of 50 nests (48 percent) in 1994, 32 of 53 nests (60 percent) in 1995, and 31 of 52 nests (59 percent) in 1996 were in predator-proof burrows.

Pairs that hatched young were provided with supplemental food for between 40 and 50 days until family groups became independent of their nest burrows. Pairs were fed at 3-day intervals, by leaving dead laboratory mice and quail in nest chambers or in burrow entrances (Wellicome 1997b). Pairs were provided with food at a rate of approximately 85 g/nest/day, corresponding to more than three times the

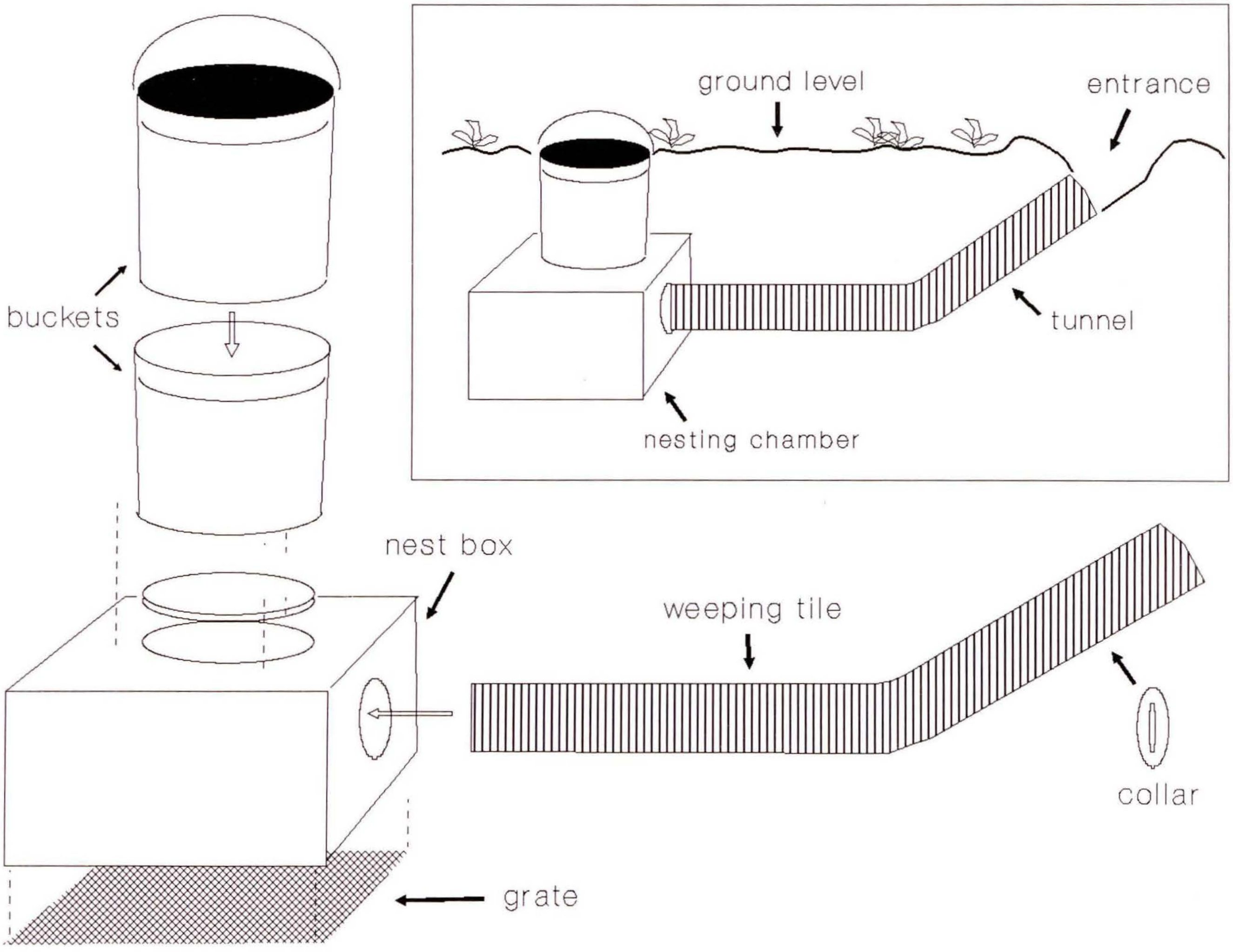

Figure 2.—*Predator-proof artificial nest burrow (ANB) used to exclude fossorial mammalian predators from Burrowing Owl (*Speotyto cunicularia*) nests in the Grassland Ecoregion of Saskatchewan. ANBs were installed to replace occupied natural burrows before egg laying each year. The bucket system enables investigators to access the nest chamber, but still provides insulation from heat or cold when the dirt-filled bucket is in place.*

food required for daily existence metabolism of an adult Burrowing Owl in captivity (mean = 26 g, Marti 1973). In 1994 and 1995, all nests active after hatch were provided with supplementary food (43 and 50 nests, respectively). In 1996, 43 nests (84 percent of active nests) were provided with extra food. Nestling survival was monitored by counting chicks inside nest chambers at 6-day intervals until fledging. For nests in natural burrows, fledglings were counted at burrow entrances during three or more 30-minute observation periods late in the nestling stage.

To determine dispersal distances, we banded all nestlings produced in artificial burrows and most fledglings from natural burrows. We captured as many adults as possible, either inside nest boxes during incubation or outside natural burrows using noose carpets baited with dead quail (Bloom 1987), and gave each adult a unique combination of colored leg-bands. A total of 157 fledglings (67 percent) and 37 adults (42 percent) were banded in 1994, 158 fledglings (87 percent) and 32 adults (31 percent) in 1995, and 187 fledglings (88 percent) and 69 adults (65 percent) in 1996. We defined adult dispersal as the straight-line distance between the breeding site at banding and the next observed breeding site in a subsequent year (Korpimäki *et al.* 1987). Although most owls were sighted in consecutive years, three individuals resighted 2 years after their initial capture were also included in the analysis. We defined natal dispersal as the distance from a bird's natal site to its first observed breeding site. Most of the owls bred first when they were 1 or 2 years of age, but some of the owls included in our analysis were not observed breeding until they were 3 or 4 years of age. Owl banding began in the study area in 1985 (D.G. Hjertaas, P.C. James, and L.Scott; unpubl. data). The oldest known-age breeders were banded as adults 4 years before their last resighting and were, thus, at least 5 years of age.

All statistical tests were performed using SYSTAT for Windows (Wilkinson 1992). Two-tailed Fisher's exact tests and Mann-Whitney U-tests were used for hypotheses concerning site fidelity and dispersal distances, respectively, because effects in either direction were of interest and dispersal distances had non-normal distributions. All other tests were one-tailed because effects in only the predicted direction were meaningful to the hypotheses tested (Sokal and Rohlf 1981). Mantel-Haenszel Chi-square was used to remove effects of year when examining the relationship between predator-proofing of burrows and frequency of nest predation.

RESULTS

Productivity

To test whether the technique of food supplementation increased the number of fledglings produced per successful nesting attempt in Burrowing Owls, we present data from 3 years in which control pairs (those not receiving extra food) existed for comparison (T.I. Wellicome, unpubl. data). Pairs that were fed during the nestling period fledged 41 percent (range: 16-192 percent) more offspring, on average, than did control pairs with only natural prey available to them (ANOVA, $P < .001$; fig. 3).

Predator exclusion in 1994 was not entirely successful because badgers were able to enter some of the ANBs. Nonetheless, 67 percent of the nests managed to fledge at least one young in that year. Of the 19 nests in 1995 that were in natural burrows, 10 (53 percent) were lost to fossorial predators, which resulted in total reproductive failures. Of the 32 nests in ANBs that same year, 18 had predation attempts but only 3 (9 percent) failed as a result of these attempts: two burrow mouths were filled in by badgers, causing death of eggs and young chicks, and one nest was depredated by a red fox kit small enough to fit past the predator collar in the tunnel (fig. 2). In 1996, none of the 31 nests in predator-proof ANBs failed because of predation, despite several attempts at six of them; whereas, 3 of 16 natural burrows (19 percent) appeared to have been depredated. Predator-proof burrows thus significantly decreased the frequency of nest predation (Mantel-Haenszel Chi-Square statistic = 17.2, $P < .001$).

The increase in the number of fledglings, due to food supplementation, and the increase in nest success, due to predator exclusion, resulted in overall productivity of 5.0, 3.6, and 4.2 fledglings per attempt in 1994, 1995, and 1996, respectively. The average productivity in years with productivity enhancement (mean = 4.3 fledglings per attempt, SD = 0.7, $N = 3$ years) was substantially higher (Student t-test, $P = .03$) than the average for pre-treatment years (1986- 1993, mean = 2.6 fledglings per attempt, SD = 1.3, $N = 8$ years).

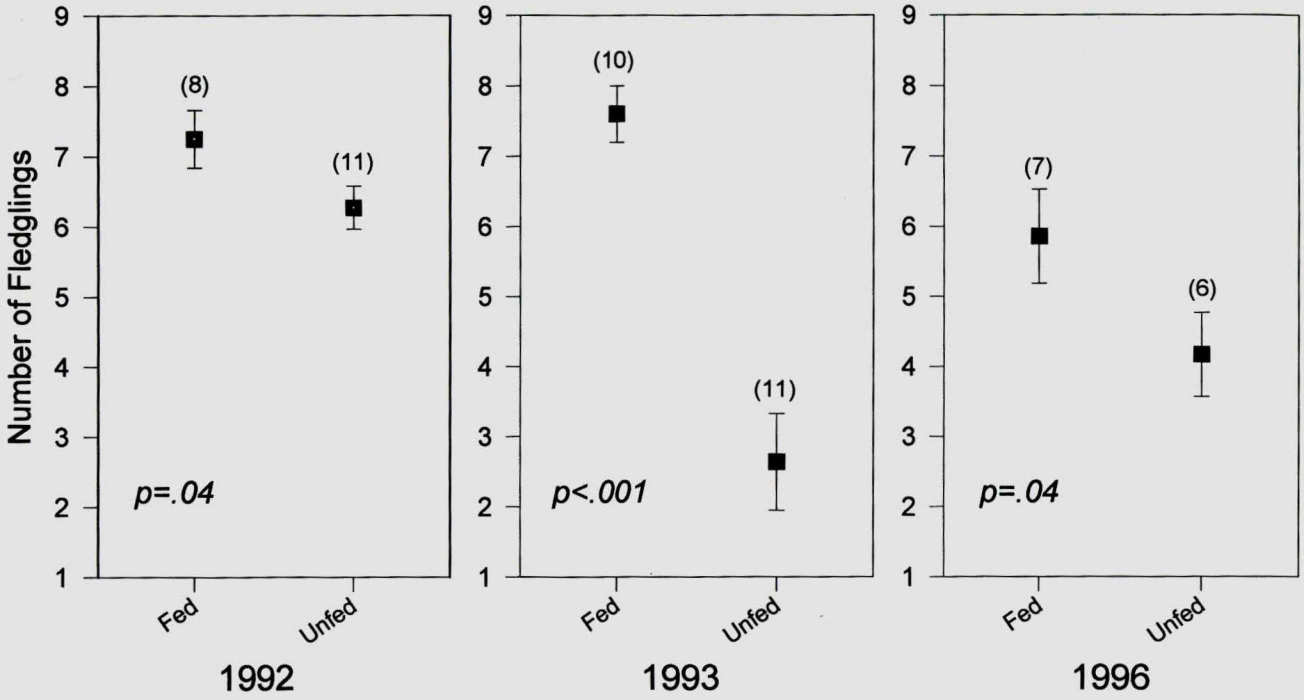

Figure 3.—*Number of young fledged per successful attempt (mean and standard error) by Burrowing Owl (*Speotyto cunicularia*) pairs provided with extra food during brood-rearing (Fed) and by control pairs not given extra food (Unfed) in the Grassland Ecoregion of Saskatchewan. Sample sizes are shown in parentheses. Fed pairs fledged significantly more young in each of the 3 years (Student's t-tests, = 0.05), although differences varied among years. 1992 and 1993 data are from earlier experiments on the same study site (Wellicome 1997b; T.I.Wellicome, unpubl. data).*

Population Change

For the northeastern portion of our study area, we compared the annual decline in percent of the population following years of productivity enhancement (1994-1996) to the annual percent decline prior to productivity enhancement (1987-1993; fig. 4). The average, annual percent decline was greater before productivity enhancement (mean = 24.7 percent, *N* = 7) than after (mean = 11.8 percent, *N* = 2). This difference was statistically significant (Student t-test with separate variances, *P* = .04).

Over the entire study area, the population showed no decline after the first year of treatment (between 1994 and 1995; fig. 5), but declined by approximately 17 percent following the second year (between 1995 and 1996).

Dispersal

Fidelity to breeding sites (dispersal distance = 0) was high for adults in general (fig. 6a), but was higher for adult males than for adult

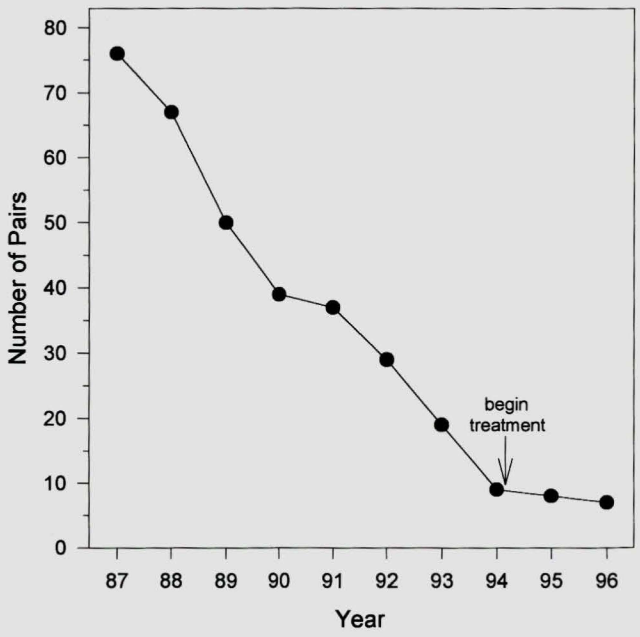

Figure 4.—*Number of Burrowing Owl (*Speotyto cunicularia*) pairs present each year in the northeastern portion of our study site in the Grassland Ecoregion of Saskatchewan. Historical data provided by Dr. Paul C. James, Saskatchewan Environment and Resource Management.*

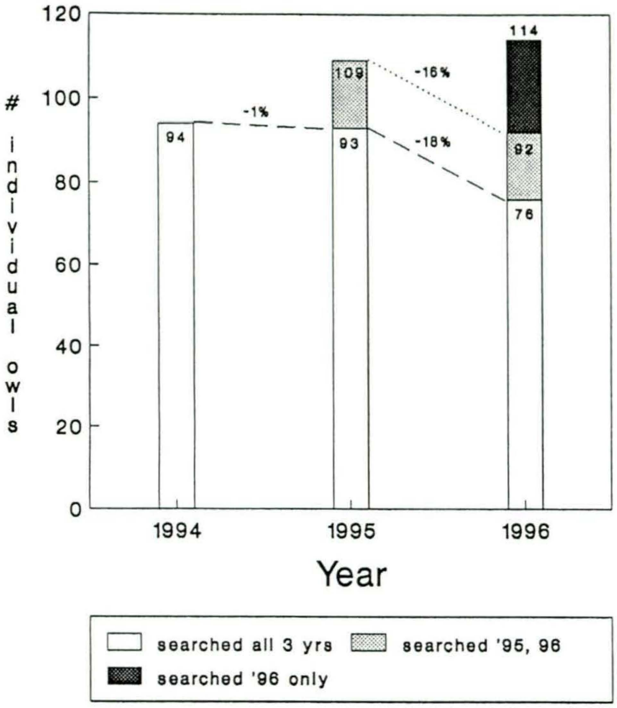

Figure 5.—*Number of individual Burrowing Owls (*Speotyto cunicularia*) in 10,000 km² Grassland Ecoregion of Saskatchewan study site in 3 years. Food supplementation and predator exclusion began for the population in 1994. The grey bars indicate owls found on land to which we were allowed access beginning in 1995. The darkest bar in 1996 represents owls found on new land searched when the study area was expanded to the south by approximately 20 percent (based on area). Although there was no decline in the study population following the first treatment year, the population declined by approximately 17 percent following the second treatment year.*

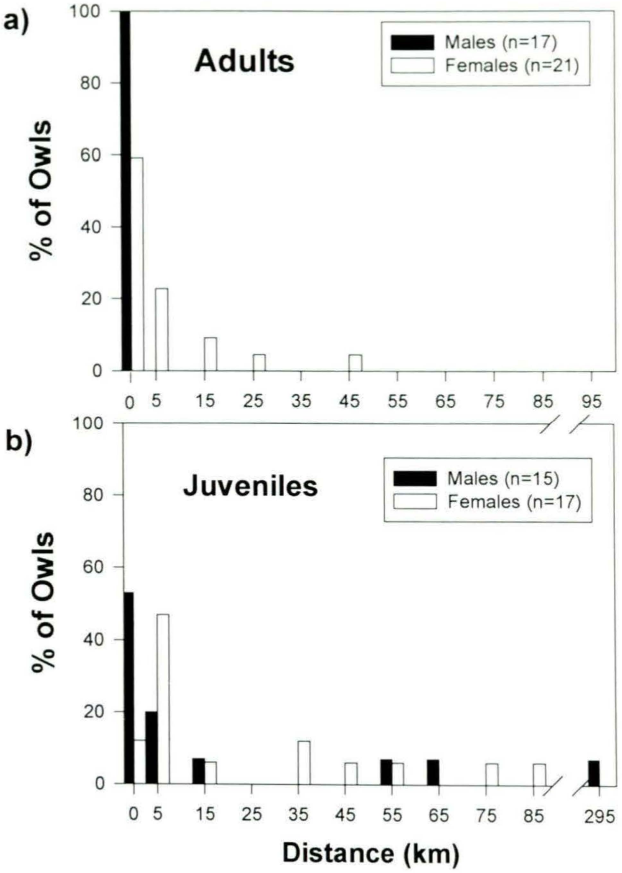

Figure 6.—*Dispersal distances (presented in 10 km blocks) for all Burrowing Owls (*Speotyto cunicularia*) captured inside the Grassland Ecoregion of Saskatchewan study area in at least 2 different years. A distance of 0 km indicates the individual was found breeding at the same site in which it was captured in a previous year. a) Breeding dispersal distances for owls trapped as adults and retrapped or sighted breeding in a subsequent year. b) Natal dispersal distances for birds banded as nestlings and returning to breed on the study site.*

females (Fisher's exact test, $N = 38$, $P = .005$). In fact, males showed absolute fidelity to their breeding sites. Consequently, adult female dispersals were of greater distance than were those of males ($U = 111$, $N = 38$, $P = .005$). A few females made medium-distance movements within the study area, the farthest of which was 49 km, but their were no long-distance movements by adults. In general, fidelity to nest sites was lower for juveniles (Fisher's Exact test, $N = 70$, $P < .001$) and they dispersed farther from nest sites than did adults ($U = 294$, $N = 69$, $P < .001$). Site fidelity was higher for juvenile males than for juvenile females (Fisher's exact test, $N = 32$, $P = .02$): over one-half of returning males bred on their natal sites, but only 12 percent of females bred on natal sites (fig. 6b). However, nearly one-half of the females settled between 1 and 10 km from their natal site. After the exclusion of one outlying male natal dispersal of 295 km, juvenile females dispersed farther on average than did males ($U = 70$, $N = 31$, $P = .05$).

The direction of dispersal showed no obvious patterns for either adult females or juveniles (fig. 7). However, the interchange of owls between sites within the study area suggests

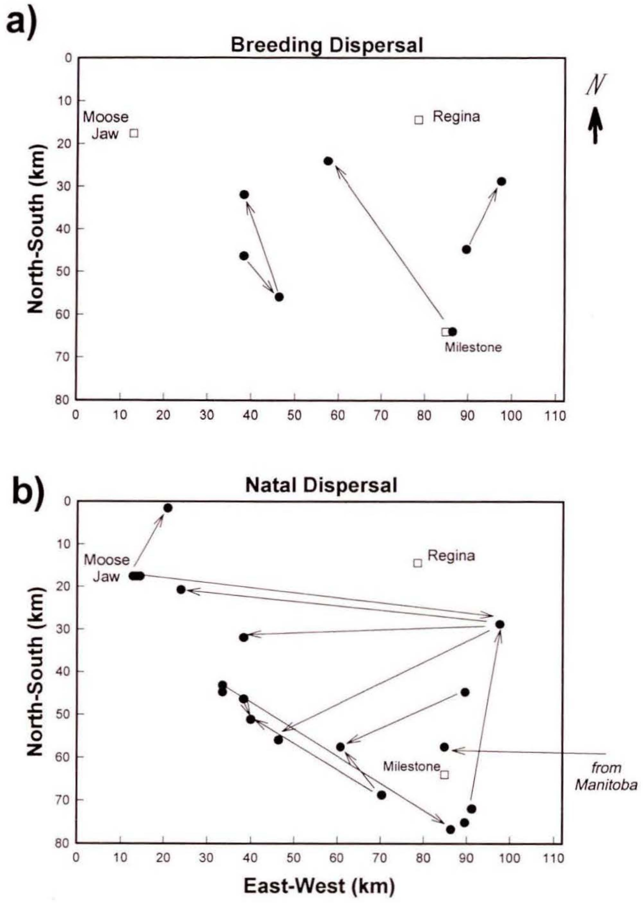

Figure 7.—*Directions and distances of between-year movements greater than 2 km in the Grassland Ecoregion of Saskatchewan. The grid represents our study area. Breeding dispersals are movements of adults and natal dispersals are movements of juveniles. Solid circles indicate Burrowing Owl (*Speotyto cunicularia*) breeding sites where dispersal occurred, and empty squares indicate cities or towns.*

that Burrowing Owl numbers on a given site are partially dependent on numbers and productivity at other sites over a large area. This is especially true for juvenile owls, whose dispersal distances were sometimes large in comparison to our study site (fig. 7b).

DISCUSSION

Dispersal distances seemed relatively large in our population, especially for juveniles. Unfortunately, there is little dispersal information available for the western Burrowing Owl with which to compare our results (Haug *et al.* 1993). Owls near Hanna, Alberta, showed dispersal patterns similar to ours, in that fidelity to breeding sites was higher in adult males than in females and adult females dispersed farther from their previous breeding sites than did males. However, the maximum breeding dispersal observed in Hanna was only 4 km (J.K. Schmutz, University of Saskatchewan, unpubl. data), compared to 49 km at our Regina site. Dispersal distances recorded in the Hanna area may have been smaller than those on the Regina Plain because habitat types differ considerably: the Hanna site is characterized by relatively continuous rangeland habitat. Dispersal distances for owls nesting in highly-fragmented agricultural land in Manitoba (De Smet 1997) were of similar magnitude to those measured in our study area.

The high nest-site fidelity of adults and the small dispersal distances relative to the size of our study area suggest that the number of adult owls emigrating from the area is quite small. However, emigration is likely frequent enough to make return rates within the study area slightly conservative estimates of adult survival. For example, the farthest adult dispersal recorded in Canada was of a Burrowing Owl banded near Saskatoon and recovered the following year, approximately 220 km to the southwest of its original breeding site (E.A. Haug, unpubl. data).

Natal site-fidelity was not high, and juvenile dispersal distances were sometimes large in relation to our study area. This may explain why we sometimes capture unbanded 1-year-old breeders in our study area (T.I. Wellicome, pers. observ.). The only banded bird known to have immigrated into our area, moved approximately 295 km from its natal site in Manitoba. Although this is the farthest natal dispersal recorded to date, it is not the first inter-provincial movement on record: a previous natal dispersal, between Manitoba and Regina (P.C. James, unpubl. data), was approximately 290 km. Such returns, coupled with the observations of natal dispersal across the breadth of our study site, suggest that there is immigration and emigration of juveniles to and from our study population. This means that any increase in the number of recruits resulting from productivity enhancement has probably occurred over a geographic area wider than our study site, thus 'diluting' the local population effect and reducing our chance of detecting a treatment-effect.

Notwithstanding the above, some of the evidence we collected suggests there has been a positive effect of our treatment on the Burrowing Owl population. In the portion of our study area that corresponds to P.C. James' historical study area, the rate of population change for the 2 years following the start of productivity enhancement was lower than in any of the 7 preceding years. Similarly, the rate of population decline for our overall study population was lower in the 2 years following productivity enhancement than it was in the 2 preceding years ('Avonlea' site in Wellicome and Haug 1995). In fact, the decline of 1 percent between 1994 and 1995 is the lowest year-to-year decline ever recorded for a Burrowing Owl population in Canada where search effort was consistent each year. On the other hand, the decline of between 16 and 18 percent from 1995 to 1996 was steep, suggesting that productivity enhancement was having little effect on the decline during that period. Our next step will be to compare the yearly rate of decline inside the study area to the rate outside the study area. For these comparisons, we plan to use data from the Operation Burrowing Owl land-owner survey for the province of Saskatchewan (see Hjertaas 1997). It will also be informative to compare, on a nest-by-nest basis, re-occupancy rates following successful and failed nesting attempts to see if probability of re-occupancy can be predicted from current nesting success (*cf.* Sonerud 1985).

For species such as the Burrowing Owl, which are precipitously declining in numbers, it is desirable to stabilize populations by slowing or halting their decline until ultimate causes can be identified and, if possible, corrected (Temple 1986). Food supplementation and predator exclusion are short-term management techniques that immediately increase Burrowing Owl reproductive output. After 2 years of post-treatment results from productivity enhancement, we cannot conclude for certain that such techniques affect population numbers, so we hesitate to make final management recommendations until our experimental population has been monitored for a few more years. If enhanced productivity does not slow the population decline, future research should focus on mortality factors during the post-fledging, migration, and wintering periods. If, however, we can demonstrate that productivity has an important influence on the study population, we can recommend specific management activities for breeding Burrowing Owls on the prairies.

Artificially increasing productivity on a prairie-wide basis can only be viewed as a 'stop-gap' option (Temple 1986)—one that may be justified in the short-term, given the severity of the problem for this species in Canada. However, such a technique is intensive and does not present a viable long-term solution. Habitat manipulations would be more effective for increasing productivity in the long term. Predation of Burrowing Owl nests could probably be decreased by increasing populations of ground squirrels, which are alternative prey for all predators of Burrowing Owls, and by increasing the size of pasture fragments. Habitat improvement, through the planting of permanent vegetation strips in highly-cultivated regions and/or rotational grazing in heavily-grazed areas, could enhance Burrowing Owl productivity by increasing cricetid prey populations.

Results from 3 years of productivity enhancement are inconclusive thus far, but are encouraging nonetheless. Data presented here are the first to suggest that manipulations of populations on the breeding grounds may slow the Burrowing Owl decline in a target area. In light of the rapid and ubiquitous erosion of Canada's Burrowing Owl population (Wellicome and Haug 1995), and the recent extirpation of the species from the province of Manitoba (K.D. De Smet, pers. comm.), we feel it important to continue productivity-enhancement experiments. Such experiments will provide direction for future research and conservation initiatives, both on and off the breeding grounds, by helping to determine whether the decline is linked ultimately to decreased productivity or to increased mortality.

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LITERATURE CITED

Bloom, P.H. 1987. Capturing and handling raptors. In: Raptor management techniques manual. Washington, DC: National Wildlife Federation: 99-123.

Butts, K.O. 1973. Life history and habitat requirements of Burrowing Owls in western Oklahoma. Stillwater, ID: Oklahoma State University. 172 p. M.S. thesis.

De Smet, K. 1997. Burrowing Owl (*Speotyto cunicularia*) Monitoring and Management Activities in Manitoba, 1987-1996. In: Duncan, J.R.; Johnson, D.H.; Nicholls, T.H., eds. Biology and conservation of owls of the northern hemisphere: 2d international symposium; 1997 February 5-9; Winnipeg, Manitoba. Gen. Tech. Rep. NC-190. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station: 123-130.

Gleason, R.S. 1978. Aspects of the breeding biology of Burrowing Owls in southeastern Idaho. Moscow, ID: University of Idaho. 47 p. M.S. thesis.

Harris, W.C.; Kabzems, A.; Kosowan, A.L.; Padbury, G.A.; Rowe, J.S. 1983. Ecological regions of Saskatchewan. Tech. Bull. 10. Regina, SK: Saskatchewan Parks and Renewable Resources. 39 p.

Haug, E.A. 1985. Observations on the breeding ecology of Burrowing Owls in Saskatchewan. Saskatoon, SK: University of Saskatchewan. 89 p. M.S. thesis.

Haug, E.A.; Millsap, B.A.; Martell, M.S. 1993. Burrowing Owl (*Speotyto cunicularia*). In: Poole, A.; Gill, F., eds. The Birds of North America, No. 61. Philadelphia, PA: The Academy of Natural Sciences; Washington, DC: The American Ornithologists' Union.

Haug, E.A.; Oliphant, L.W. 1990. Movements, activity patterns, and habitat use of Burrowing Owls in Saskatchewan. Journal of Wildlife Management. 54: 27-35.

Hjertaas, D.G. 1997. Operation Burrowing Owl in Saskatchewan. The Burrowing Owl: its biology and management: including the proceedings of the 1st International symposium; 1992 November 13-17; Bellevue, WA. In: Raptor Research Reports. Raptor Research Foundation; 9: 112-116.

Hjertaas, D.G.; Brechtel, S.; De Smet, K.D.; Dyer, O.; Haug, E.A.; Holroyd, G.L.; James, P.C.; Schmutz, J.K. 1995. National recovery plan for the Burrowing Owl in Canada. RENEW Rep. 13. Ottawa, ON: Canadian Department of the Environment, Recovery of Nationally Endangered Wildlife Committee. 33 p.

James, P.C. 1992. Where do Canadian Burrowing Owls spend the winter? Blue Jay. 50(2): 93-95.

James, P.C.; Ethier, T.J.; Toutloff, M.K. 1997. Parameters of a declining Burrowing Owl population in Saskatchewan. The Burrowing Owl: its biology and management: including the proceedings of the 1rst International symposium; 1992 November 13-17; Bellevue, WA. In: Raptor Research Reports. Raptor Research Foundation; 9: 34-37.

James, P.C.; Fox, G.A. 1987. Effects of some insecticides on productivity of Burrowing Owls. Blue Jay. 45: 65-71.

James, P.C.; Fox, G.A.; Ethier, T.J. 1990. Is the operational use of strychnine to control ground squirrels detrimental to Burrowing Owls? Raptor Research. 24: 120-123.

Korpimäki, E.; Lagerstrom, M.; Saurola, P. 1987. Field evidence for nomadism in Tengmalm's Owl *Aegolius funereus*. Ornis Scandinavica. 18: 1-4.

Marti, C.D. 1973. Food consumption and pellet formation rates in four sympatric owl species. Wilson Bulletin. 85: 178-81.

Martin, T.E. 1992. Interaction of nest predation and food limitation in reproductive strategies. Current Ornithology. 9: 163-197.

McNamara, J.M.; Houston, A.I. 1987. Starvation and predation as factors limiting population size. Ecology. 68(5): 1515-1519.

Schmutz, J.K.; Wood, G.; Wood, D. 1991. Spring and summer prey of Burrowing Owls in Alberta. Blue Jay. 49: 93-97.

Sokal, R.R.; Rohlf, F.J. 1981. Biometry. 2d ed. New York, NY: W.H. Freeman and Co. 859 p.

Sonerud, G.A. 1985. Nest-hole shift in Tengmalm's Owl *Aegolius funereus* as defense against nest predation involving long-term memory in the predator. Journal of Animal Ecology. 54: 179-192.

Temple, S.A. 1986. The problem of avian extinctions. Current Ornithology. 3: 453-485.

Wedgwood, J.A. 1978. The status of the Burrowing Owl in Canada. A report prepared for the Committee on the Status of Endangered Wildlife in Canada. Ottawa, ON: Canadian Wildlife Service. 82 p.

Wellicome, T.I. 1997a. Status of the Burrowing Owl (*Speotyto cunicularia hypugaea*) in Alberta. Wildl. Status Rep. 11. Edmonton, AB: Alberta Environmental Protection, Wildlife Management Division. 21 p.

Wellicome, T.I. 1997b. Reproductive performance of Burrowing Owls (*Speotyto cunicularia*): effects of supplemental food. The Burrowing Owl: its biology and management: including the proceedings of the 1st International symposium; 1992 November 13-17; Bellevue, WA. In: Raptor Research Reports. Raptor Research Foundation; 9: 68-73.

Wellicome, T.I.; Haug, E.A. 1995. Second update of status report on the Burrowing Owl, *Speotyto cunicularia*, in Canada. Committee on the Status of Endangered Wildlife in Canada, Canadian Wildlife Service, Ottawa, ON. 37 p.

Wilkinson, L. 1992. SYSTAT for Windows: Version 5. SYSTAT, Evanston, Illinois, USA.

Zarn, M. 1974. Burrowing Owl (*Speotyto cunicularia hypugaea*). Habitat management series for unique or endangered species. Rep. No. 11. T-N-250. Denver CO: U.S. Department of the Interior, Bureau of Land Management, Denver Service Center. 25 p.

Great Gray Owl (*Strix nebulosa*) Breeding Habitat Use Within Altered Forest Landscapes

Michael B. Whitfield and Maureen Gaffney[1]

Abstract.—We investigated Great Gray Owl (*Strix nebulosa*) habitat use in eastern Idaho and northwestern Wyoming. Great Gray Owls were not found in severely altered habitats, but young were fledged in areas where 17 to 26 percent of formerly continuous forest had been clearcut. Average clutch (2.7) and brood (2.3) sizes were comparable to other populations, whereas juvenile mortality in the first 60 days post-fledging may have exceeded 60 percent. Habitat features were measured at independent owl activity locations, and compared pairwise with measurements at associated random points. Fledged juveniles selected micro-habitats with greater cover than was found at random locations.

Through intensive searches in 1979-1983, Franklin (1987, 1988) documented a productive population of Great Gray Owls in the eastern Idaho/northwest Wyoming portion of the Greater Yellowstone Ecosystem. Most nesting pairs were found within the lodgepole pine/Douglas fir/aspen zone, where pocket gophers (*Thomomys talpoides*) were the predominant prey. Groves and Zehntner (1990) did not find Great Gray Owls at historic nesting areas during 1989 surveys of the area, and suggested that Great Gray Owl numbers within the study area may have declined due to timber harvest. However, despite the Great Gray Owl's relatively large size and bold nature, Great Gray Owl habitat use remains poorly understood (Duncan and Hayward 1994). Our project was undertaken to enhance current knowledge of the conservation needs of Great Gray Owls and their habitats in southeast Idaho and northwestern Wyoming. The objectives of our ongoing study are: (1) to document productivity at selected great gray breeding areas as a baseline for long-term monitoring; (2) to learn adult and juvenile habitat use relationships within breeding areas; and (3) to determine juvenile survival parameters.

STUDY AREA

This study was conducted from 1994-1996 in southeastern Idaho and northwestern Wyoming on the Targhee National Forest and nearby private lands. We focused on known and suspected Great Gray Owl habitat in montane forests in the foothills of the mountains that surround Teton Valley. This rural mountain basin is on the Idaho/Wyoming border approximately 24 km south of Yellowstone National Park and within the Greater Yellowstone Ecosystem. We also monitored nest sites within the southern portion of the Island Park cauldera approximately 60-80 km north of Teton Valley, and in the foothills of the Big Hole Mountain Range 40 km west of the valley. Whereas most of the known Great Gray Owl nests in the study area occur within or near National Forest, wintering habitat is found on private lands in the cottonwood riparian corridors in the valley bottom (Franklin 1987).

Conifer forested foothills at 2,130 to 2,440 m elevation are found around three sides of Teton Valley. These foothills lead into three mountain ranges: the Big Holes to the west, Snake River Range to the south, and the Tetons to the east. Our study area extends west across foothill areas on the north end of the Big Holes into Madison County, Idaho. Forested stands in these foothill areas are a mixture of Douglas fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*) and aspen (*Populus tremuloides*), with

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Englemann spruce (*Picea englmannii*), alpine fir (*Abies lasiocarpa*) forests at higher elevations.

The southern portion of the Island Park cauldera within the Ashton Ranger District features relatively flat expanses of lodgepole pine forest at elevations of 1,828 to 1,950 m. Forest stands also include pockets of Douglas fir, subalpine fir, and aspen. Most mature lodgepole stands within the study area, particularly in the Island Park cauldera, have been clearcut in the past 25 years, and most clearcuts have been planted to lodgepole. Soon after planting, most plantations are treated with strychnine to reduce populations of northern pocket gophers.

METHODS

We attempted to identify a baseline of great gray breeding area success and habitat use within the study area through careful compilation of recorded observations and survey results, and interview of private land owners. Breeding areas are defined as sites where adults laid eggs. A 1989 study (Groves and Zenhtner 1990) conducted a similar effort for the entire northeast portion of the Targhee National Forest. To examine general trends, we focused our extensive surveys on a smaller portion of the Targhee, the Teton Basin District. We hoped to thus assure more complete review of records and subsequent ground searches.

We located owls during early morning or late evening surveys, including use of taped calls when appropriate (Bull and Henjum 1990). Known historic sites and potential habitats within the study area were visited. Because great gray nest site fidelity is reportedly high (Bull and Henjum 1990), and average nesting home range was 4.5 km^2 (Bull *et al.* 1988, Bull and Henjum 1990) or less (e.g., Craighead and Craighead 1956), we surveyed all historic areas by walking grids within a 2 km by 2 km grid plotted around the last-known nest or location where owls were heard. Late summer we revisited areas where nests had not been located to search for fledged broods.

In 1994 we did not determine clutch size, but in 1995-1996 we recorded clutch size with a mirror pole. In all 3 years, we monitored nesting success by weekly visits to known nests. Young were banded with Fish and Wildlife Service metal bands immediately before or after fledging, and plastic-coated nylon ribbons with unique symbols were attached to the bands according to a protocol developed by Robert Nero (1980). We attempted to monitor juvenile broods from fledging until independence, when the owlets began to catch their own food. In the discussion below, the fledged, flightless period is approximately 12 days when young owls climb up trees and glide rather than fly, and independence is arbitrarily defined as 90 days post-fledging, an age when young owls are beginning to hunt for themselves (Bull and Henjum 1990). In the 1994 and 1995 breeding seasons, we tagged a total of 10 juveniles and 2 adults with 5-gm tarsal transmitters (Advanced Telemetry Systems, model 357) designed to be shed without the need for recapture. We monitored owls visually in 1996. Juveniles were captured by hand before they became capable fliers, and adults were captured with a bal chatris.

Habitat features were measured at great gray activity centers and at associated random sample points. Activity centers included nest sites, prey capture sites, and adult and juvenile perches where use was independent of observer effects. Random points were located 50 m from the activity site at a randomly selected compass bearing. By convention, the identified perches were those where birds were first located during independent, randomly selected observations. At a given site, observations were usually made twice each week. Measured habitat features at each point included perch characteristics, distance from forest edge, tree basal area as measured with a relaskop (20 factor prism, USDA Forest Service 1984), and habitat type as determined by the protocol of Steele *et al.* (1983). Additional features were measured as an average of measurements taken at four point centers 4.6 m from the activity point in the four cardinal directions. These features included: tree canopy area as a percentage measured with a densiometer, shrub layer, grass and forb canopy cover as percentages (Daubenmire 1959), and the total number of pocket gopher push piles seen within the plot circle (plot area = 65.7 m^2) intersected by the four point centers. We compared features at activity centers and random associated points through the two-tailed paired-sample t test (Zar 1974). We chose $P = 0.05$ as the level of significance.

RESULTS

Reproduction

We monitored productivity for 19 Great Gray broods, nine of which were first detected post-fledging (table 1). Hatch dates ranged from 28 May to 20 June. Clutch checks were completed with a mirror pole near hatching. Assuming a 36-day incubation period (Mikkola 1983), incubation was initiated between approximately 22 April and 15 May. Fledging occurred from 15 June to 15 July.

Table 1.—*Known productivity at monitored Great Gray Owl (*Strix nebulosa*) nesting areas in southeastern Idaho and northwestern Wyoming, 1994-1996.*

Productivity parameter	N	Average	SD	Range
Clutch size	6	2.67	0.82	2-4
Pre-fledge brood size	10	2.30	0.67	1-3
Fledged, pre-flight brood size	12	2.33	0.65	1-3
Flying brood size	19	2.16	0.50	1-3

Juvenile Survivorship Pre-Independence

We did not check clutch size until near hatching, and in most cases initiated our monitoring of juveniles at fledging. In limited monitoring of nestlings, 82.4 percent survived from hatching to fledging (n = 17). In monitoring of fledglings, 80.0 percent survived from fledging to flight (n = 30). Of the monitored juveniles that survived to flight stage (n = 24), 25.0 percent (6) were known to survive to near independence. We detected mortality of 20.9 percent (5), and lost track of 54.1 percent (13). Thus, among the monitored fledglings with known outcome (n = 17), a fledged juvenile had a 35.0 percent probability of survival to near independence. This survival estimate, a minimum, was affected by our inability to track many advanced juveniles. In 1994, transmitters unexpectedly began to fail at 40 days. Of six radio-tagged juveniles in 1994, three survived to near independence, one died, and two were lost. In 1995, all four radio-tagged juveniles were killed, the last one by humans at 72 days post-fledging. The longest we monitored any juvenile was 91 days post-fledging. Over the 3 years, 16 additional juveniles in seven broods were first located after they had attained flight. Of these, seven (44 percent) were tracked to near age of independence, with unknown outcome for the others.

In total, we noted 11 post-fledging mortalities, including, by cause: predation by Great Horned Owl (2), predation by pine marten (1), starvation (1), collision injury (2), shot by human (1), unknown causes (4).

Nest Microhabitats

Eleven different active nests were monitored within eight breeding areas, with 2 years of nesting in three of these nests. Of these, nine nests were built by goshawks (*Accipiter gentilis*) (five in Douglas fir, three in lodgepole pine, one in aspen), one by a red-tailed hawk (*Buteo jamaicensis*) (lodgepole pine snag), and one was atop a lodgepole snag. Three persisting historic nests were used in recent years; one on a Douglas-fir snag, one in a mistletoe whorl in a Douglas fir, and another in an old red-tailed hawk nest in an aspen, were not used during this study. At 10 nest sites where habitat parameters were measured, average nest tree d.b.h. was 43.6 cm (SD 18.631, Range = 23.9 - 81.8 cm), average nest height was 19.7 m (SD 6.055, Range = 7.3 - 30.2 m), average tree canopy cover was 70.6 percent (SD 25.54, Range = 29.5 - 99.0 percent), and average shrub canopy cover beneath nests was 17.2 percent (SD 19.50, Range = 0 - 54.4 percent).

Breeding Area Macro-habitats

We noted considerable habitat variation among the great gray breeding areas we monitored (table 2). We describe habitats found in three great gray breeding areas to display the range of habitats in sites where young were fledged.

At Eccles Butte, broods of three and two young fledged in 1994 and 1995 respectively. Fledglings appeared to be stressed by heat in this area, as evidenced by lethargy and panting. There was relatively little thermal cover beneath relatively thin canopied, short lodgepole pine. Great Horned Owls (*Bubo virginianus*) also used this area, and predated upon at least

Table 2.—*Great Gray Owl (*Strix nebulosa*) breeding area macro-habitat features in eastern Idaho and northwestern Wyoming.*[1]

Breeding area	Dominant tree species[2]	Percent openings	Average percent tree canopy cover	Average percent shrub canopy cover
Bustle Creek	DF	<15	60.0	24.1
Dry Hollow	DF	<15	75.6	28.4
Dry Ridge 1	LPP	20	51.4	26.6
Dry Ridge 3	LPP	20	44.7	21.6
Eccles Butte	LPP	56	37.0	0.2
Grandview	DF	<10	72.0	10.4
Hatchery Ford	LPP	56	28.1	0.1
Pole Canyon	DF	26	64.0	31.9

[1] Habitat features measured at randomly selected locations within forest stands, except for percent openings, which is a total percentage for a habitat circle of 5 km^2 around known nest sites.

[2] DF = Douglas fir (*Pseudotsuga menziesii*), LPP = lodge pole pine (*Pinus contorta*).

one juvenile great gray. From 1980-1987, 56 percent of the forest in this area was clearcut, and clearcuts were treated for pocket gophers (last treatment in 1992). Tree canopy cover at random sites averaged 37 percent, (n = 8, SD = 15.900). The forested area featured less than 1 percent shrub cover, and an average of 4.3 gopher pushpiles/plot (n = 18, SD = 6.685). Clearcuts featured very high densities of gophers. Nest sites used in this area in 1994 (top of lodgepole snag) and 1995 (red-tailed hawk nest in dead lodgepole) averaged 48.1 percent tree canopy cover (SD = 26.929). No owls were found here in 1996.

At Dry Ridge, two broods were fledged in 1994 (1.5 young/brood), and three in 1996 (2 young/brood). We detected no mortalities, although we suspected as many as four given the disappearance of parts of broods before independence. Great Horned Owls nested in the lower elevations of the area, and goshawks were also seen. Clearcuts and openings over the broad area where these owls were found (approximately 1,850 ha) represented 20 percent of the area. Tree canopy cover averaged 51.4 percent (n = 27, SD = 14.904). Gopher pushpiles averaged 2.1/plot (n = 75, SD = 3.904) within the forested area, with much higher densities observed in clearcuts.

In the Grandview breeding area, broods of two, three, and one fledged successfully in 1994-1996, respectively. One fledged juvenile died of starvation at 16 days post-fledging and another was eaten by a Great Horned Owl at 51 days post-fledging. A goshawk pair nested successfully near the great grays each year, and often interacted with the owls, striking the adult female during three observation periods. Great Horned Owls also nested in the area. This area features expansive Douglas fir forest with few openings at the edge of large natural meadows. Tree canopy cover averaged 72.0 percent (n = 20, SD = 14.553). Gopher pushpiles within the Douglas fir forest averaged 1.9/plot (n = 34, SD = 3.440).

Juvenile Owl Habitat Use

Juveniles generally selected perch sites in areas that featured greater tree canopy cover than was found in associated random plots. In three of four areas with adequate sample size, we rejected the null hypothesis that juveniles did not select areas with different canopy cover than available randomly (table 3). Juveniles appeared selective for multiple factors correlated with tree canopy cover, but the differences were not significant at the level selected. They appeared to select areas with greater basal area than found in random samples, and less canopy cover in understory shrubs, grasses and forbs.

Juveniles usually perched at least 15 m away from the edges of clearcuts or natural openings (table 4). We did not group these data among breeding areas because of the differences in habitat. For example, at the Grandview breeding area, which features nearly continuous, mature Douglas fir, the juveniles perched

Table 3.—*Tree canopy cover (as a percentage) at juvenile Great Gray Owl (*Strix nebulosa*) perch sites and random sites in four breeding areas in eastern Idaho/western Wyoming, 1994-1996.*

Breeding area	**Can. cover**		**Paired-sample t test statistics**				**Test result**
	Mean	**SD**	**n[1]**	**Ave. d[2]**	**SE**	**t value**	
Dry Ridge 1							
Juveniles	62.3	11.798	27	10.8	4.105	2.643	p = 0.015 reject Ho[3]
Random	51.4	14.904					
Pole Canyon							
Juveniles	56.2	22.065	16	7.7	6.366	1.216	p = 0.258 do not reject Ho
Random	64.0	13.396					
Grandview							
Juveniles	82.0	9.586	20	9.8	3.874	2.527	p = 0.021 reject Ho
Random	72.0	14.553					
Bustle Creek							
Juveniles	76.7	12.905	22	16.7	5.073	3.285	p = 0.004 reject Ho
Random	60.0	22.074					

[1] n = number of paired samples, habitat features at observed owl activity locations during independent, randomly selected observation periods compaired to associated, randomly selected sample points (see methods).

[2] The average d is the mean difference between paired measurements of percent canopy cover.

[3] Ho = canopy cover not significantly different.

Table 4.—*Distance (m) of juvenile Great Gray Owl (*Strix nebulosa*) perches to edge of nearest opening during the pre-independence period, eastern Idaho/western Wyoming, 1994-1996.*

Breeding area	**Average**	**SD**	**n[1]**
Dry Ridge 1	17.2	22.104	27
(Lodgepole pine forest, 20 percent of area in clearcuts and natural openings.)			
Pole Canyon	36.0	38.986	14
(Mixed Douglas fir/lodgepole pine forest, 26 percent of area in clearcuts and natural openings.)			
Grandview	130.4	482.505	22
(Nearly continuous mature, open-grown Douglas fir at lower edge of treeline, bordered by expansive natural meadow and brushfields.)			
Bustle Creek	17.3	14.471	19
(Nearly continuous mixed Douglas fir/lodgepole pine forest, with many small natural openings.)			
Eccles Butte	16.6	16.512	8
(Lodgepole pine forest, 56 percent of area in clearcuts)			

[1] n = number of independent juvenile owl relocations per breeding area during independent, randomly selected observation periods.

relatively far from openings throughout the monitoring period. At most areas, particularly where there were many clearcuts with large pocket gopher populations, the juveniles moved closer to openings as they matured. Advanced juveniles at near independence sometimes flew into clearcuts to intercept the adult male returning with prey.

Flighted juveniles ($n = 143$ independent observations) beyond 12 days after fledging perched higher in the concealment and thermal cover of the tree canopy than did younger juveniles ($n = 53$) ($p < 0.001$). Average perch height for the young juveniles was 5.3 m (SD = 3.002), versus an average perch height of 8.5 m (SD = 4.274) for flighted juveniles. Flighted juveniles also perched significantly higher in the canopy than adults ($n = 94$), whose average perch height was 5.2 m (SD = 2.982).

As juveniles neared independence, they perched at heights more similar to those of adults. Adults were often seen perched at clearcut edges, and sometimes within clearcuts on stumps or small trees. Observed adult prey capture attempts ($n = 59$) occurred in clearcuts or natural openings in 61 percent of observations. Pocket gophers were the prey most often (48 of 82 prey deliveries where prey species were determined) delivered to young in all but the heavily forested Bustle Creek area, where *Microtus* spp. were more frequently taken.

Current Breeding Activity in Historical Breeding Areas

Franklin (1987, 1988) and other observers were interviewed by Groves and Zehntner (1990) to document historical great gray nesting sites in 24 areas on the Targhee National Forest, including four areas on the Teton Basin District. None of the Teton Basin areas were known to be active after 1986. In 1989, Groves and Zehntner (1990) found no active nests, but documented observations of adults or fledged young in six locations in the Teton Basin area.

The incidental records and timber sale survey results we reviewed for Teton Basin did not represent systematic surveys and were too incomplete to yield productivity or trend data. However, they did document multiple years of Great Gray Owl occupancy of at least 16 distinct breeding areas in the breeding season, areas we labeled historic breeding areas, with historic nesting success detected in 13 areas. Multiple breeding pairs were documented in three of these areas.

We separated historic breeding areas into three categories based upon the percentage of area clearcut (table 5). Over the past 14 years, clearcutting of mature forest (lodgepole and Douglas fir) has occurred in nine of the 16 areas we examined on the Teton Basin District. No owls were detected in the four cut-over areas where an average of 49.3 percent of mature forest was cut (estimated habitat circle of 5 km^2, clearcut area range = 39 - 62 percent, SD = 11.68). In four of the five cut-over areas with more intact habitat, we saw or heard adult great grays (average area clearcut plus natural openings = 20.8 percent, range = 14 - 26 percent, SD = 5.124). We detected successful nesting in two of these areas. In one of the two areas, at least three breeding pairs successfully fledged young in 1996. Successful great gray nesting was observed in four of the seven nesting areas where only minor timber harvest has occurred.

Table 5.—*Current use of historic Great Gray Owl* (Strix nebulosa) *breeding areas in the Teton Basin area, eastern Idaho and northwestern Wyoming, 1994-1996.*

Percentage of breeding area in openings	Total number of known historical areas	Number of historical areas currently active
Clearcut area Average 49.3 percent Range = 39-62 percent	4	0
Clearcut area Average 20.8 percent Range = 14-26 percent	5	4
Minimal timber harvest Openings < 15 percent of area	7	4

We also monitored great gray broods in two areas, Hatchery Ford (two broods in 1994) and Eccles (one brood in 1994, one brood in 1995), on the Ashton District in the Island Park caldera. In these areas, 56 percent of the mature forest has been clearcut, and similar cutting intensity, followed by planting and pocket gopher control, has occurred over broad areas of the District. Although we detected no immediate effect on fledged broods during tree planting and extensive gopher control at Hatchery Ford in 1994, we did not find great grays in the area in 1995-1996. We found no owls at Eccles in 1996.

DISCUSSION

Reproduction and Juvenile Survivorship

Franklin (1987) found a mean clutch size of 3.3 eggs, a mean brood size of 3.0, mean fledgling group size of 3.0, and mean group size of 2.0 when flight was attained. These clutch and brood sizes were statistically similar to those found for other studies in North America (Duncan and Hayward 1994), but smaller than reported for Scandinavia. Our clutch (2.7) and nestling (2.3) brood sizes were smaller than Franklin (1987) found in this area, but within the range expected in North America.

Franklin (1988) reported that a young great gray had a survival probability of 0.76 through incubation as an egg (n = 25), 0.89 survival probability from hatching to fledging (n = 19), and 0.77 survival probability from fledging to flight stage at approximately 14 days post-fledging (n = 13). Bull *et al.* (1989) noted that nine of 33 radio-tagged juveniles in Oregon died before independence. Bull *et al.* (1989) also reported that juveniles had a 0.53 probability of surviving their first 12 months. High mortality of juveniles once they leave their natal area, at independence, may be attributable to inexperience (Duncan 1987). Starving young owls may be less wary of predators and more intent on foraging, and unfamiliarity with a new habitat puts them at a disadvantage when faced with that habitat's predators.

Our small sample sizes and lack of a population estimator prevent a clear estimate of juvenile mortality. However, the high mortality we observed before independence is cause for concern given that additional mortality might be expected when juveniles become independent of adults. Some of the more severely altered habitats may have become ecological traps for breeding Great Gray Owls; these areas have abundant prey but insufficient cover to ensure that adequate numbers of juveniles survive. Juvenile mortality is of far less concern than adult mortality for relatively long-lived species such as Great Gray Owls, but could limit population sustainability if too extreme. Further study is needed to determine conclusively if habitat alterations have resulted in increased juvenile mortality.

Habitat Use

Of 15 nests that Franklin (1987, 1988) monitored in our region, 60 percent were in broken-topped snags and 40 percent on stick nest platforms, primarily nests built by accipiters. In our study, we found a shift to more stick nests (91 percent of active nests). Fewer older growth snags are currently available, in part because of stem age and firewood cutting.

Our habitat selection study suggests that juvenile great grays require security cover. We measured habitat features at random points close enough to activity points to be within similar habitat. This allowed us to detect selectivity for denser canopy cover than found at random sites. Bull and Henjum (1990) reported that owlets remained in forests with at least 60 percent canopy closure.

There were not statistically detectable differences between activity locations and random points for more general features such as slope or slope aspect; our random points were near enough to the activity points as to usually be within the same slope. However, monitored great grays avoided steep slopes, particularly northern exposures which are heavily covered with shrub understory in our locale. They also avoided dense, young stands of lodgepole pine in plantations.

Basal area did not prove to be an indicator of habitat selectivity, but in review, this measurement has little meaning unless coupled with stem density and size. We are attempting to develop a better index of features that may be important to Great Gray Owls.

Over the broader landscape, Great Gray Owls in our study area may have demonstrated considerable adaptability to habitat alteration. However, removal of over 50 percent of forest cover may eliminate great gray production in traditional nesting areas. One important factor may be that primary stick nest builders, e.g., goshawks, may have lesser tolerance to habitat alteration than the owls, and thus not provide nest structures. We also suspect that juvenile great gray mortality may be greater in these habitats. Our ongoing investigation of the landscape ecology of Great Gray Owls in eastern Idaho, northwestern Wyoming is in a preliminary stage.

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LITERATURE CITED

Bull, Evelyn L.; Henjum, M.G.; Rohweder, R.S. 1988. Home range and dispersal of Great Gray Owls in northeastern Oregon. Journal of Raptor Research. 22: 107-115.

Bull, Evelyn L.; Henjum, M.G.; Rohweder, R.S. 1989. Reproduction and mortality of Great Gray Owls in Oregon. Northwest Science. 63: 38-48.

Bull, Evelyn L.; Henjum, M.G. 1990. Ecology of the Great Gray Owl. Gen. Tech. Rep. PNW-265. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 39 p.

Craighead, John J.; Craighead, F.C. 1956. Hawks, owls and wildlife. Harrisburg, PA: Stackpole Co. and Washington, DC: Wildlife Institute.

Daubenmire, Rexford. 1959. A canopy-coverage method of vegetation analysis. Northwest Science. 33: 43-64.

Duncan, James R. 1987. Movement strategies, mortality, and behavior of radio-marked Great Gray Owls in southeastern Manitoba and northern Minnesota. In: Nero, R.W.; Clark, R.J.; Knapton, R.J.; Hamre, R.H., eds. Biology and conservation of northern forest owls: symposium proceedings; 1987 February 3-7; Winnipeg, MB. Gen. Tech. Rep. RM-142. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 101-107.

Duncan, James R.; Hayward, P.H. 1994. Review of technical knowledge: Great Gray Owls. In: Hayward, G.D.; Verner, J., eds. Flammulated, Boreal, and Great Gray Owls in the United States: a technical conservation assessment. Gen. Tech. Rep. RM-253. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 159-175.

Franklin, Alan B. 1987. Breeding biology of the Great Gray Owl in southeastern Idaho and northwestern Wyoming. Humboldt, CA: Humboldt State University. 83 p. M.S. thesis.

Franklin, Alan B. 1988. Breeding biology of the Great Gray Owl in southeastern Idaho and northwestern Wyoming. Condor. 90: 689-696.

Groves, Craig; Zehntner, E. 1990. Distribution and status of Great Gray Owls (*Strix nebulosa)* on the Targhee National Forest. Cooperative study between the Targhee National Forest/Idaho Department of Fish and Game P.O. No. 40-02S0-9-0690. 66 p.

Mikkola, Heimo. 1983. Owls of Europe. Vermillion, SD: Buteo Books. 397 p.

Nero, Robert W. 1980. The Great Gray Owl-phantom of the northern forest. Washington, DC: Smithsonian Institution Press. 167 p.

Steele, Robert; Cooper, S.V.; Ondov, D.M.; Roberts, D.W.; Pfister, R.D. 1983. Forest habitat types of eastern Idaho-western Wyoming. Gen. Tech. Rep. INT-144. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 122 p.

USDA Forest Service. 1984. Silviculture examination and prescription handbook. Forest Service Manual 2409.26d Chapter 10.

Zar, J.H. 1974. Biostatistical analysis. Englewood Cliffs, NJ: Prentice-Hall, Inc. 620 p.

Conservation Implications of a Multi-scale Study of Flammulated Owl (*Otus flammeolus*) Habitat Use in the Northern Rocky Mountains, USA

Vita Wright, Sallie J. Hejl, and Richard L. Hutto[1]

Abstract.—Our multi-scale analysis of Flammulated Owl (*Otus flammeolus*) habitat use in the northern Rocky Mountains indicates some landscapes may be unsuitable for this species. As a result, there may be less habitat available for Flammulated Owls than thought based on the results of microhabitat studies. Thus, we suggest Flammulated Owl habitat conservation measures be based on the results of landscape-level, as well as microhabitat studies. Habitat conservation and restoration efforts in the ponderosa pine ecosystem should retain large trees, large snags, understory tree thickets, and grassland openings within landscapes that contain an abundance of suitable forest types.

Effective conservation strategies cannot be designed without understanding the distributions of rare species. Bird distributions are heavily dependent on habitat distribution (reviews in Cody 1985), partly because populations are limited by the availability of suitable habitat. Thus, identifying and maintaining adequate amounts of suitable habitat are critical to supporting population sizes and structures necessary for long-term species viability.

Flammulated Owls (*Otus flammeolus*) in the central Rocky Mountains (Hayward 1986, Reynolds and Linkhart 1992) and Blue Mountains (Bull *et al.* 1990) predominantly nest and forage in old-growth ponderosa pine (*Pinus ponderosa*) forests, suggesting the species depends on the ponderosa pine ecosystem for population viability in some geographic areas. This ecosystem has been heavily altered by past forest management in the northern Rocky Mountains. Specifically, the removal of overstory ponderosa pine since the early 1900's and nearly a century of fire suppression have led to the replacement of most old-growth ponderosa pine forests by younger forests with a greater proportion of Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) than ponderosa pine (Habeck 1990). Clearcut logging and subsequent reforestation have converted many older stands of ponderosa pine/Douglas-fir forest to young structurally-simple ponderosa pine stands (Wright and Bailey 1982).

Fire scar evidence in the northern Rocky Mountains indicates that ponderosa pine forests burned approximately every 1-30 years prior to fire suppression, preventing contiguous understory development and, thus, maintaining relatively open ponderosa pine stands (Arno 1988, Habeck 1990). In old forests that retain a ponderosa pine overstory, a century of fire exclusion has permitted development of a more contiguous dense Douglas-fir understory (Mutch *et al.* 1993). USDA Forest Service personnel entrusted with the management of national forests in the northern Rocky Mountains are currently investigating techniques to remove understory Douglas-fir and return pre-European-settlement fire regimes to ponderosa pine ecosystems (Mutch *et al.* 1993). National Forests such as the Bitterroot and Lolo National Forests in west-central Montana are proposing to restore old-growth ponderosa pine forests by removing Douglas-fir from mixed ponderosa pine/Douglas-fir stands to increase the proportion of ponderosa pine trees relative to Douglas-fir, and to thin the Douglas-fir understory. Alteration of forest conditions can be expected to change the bird communities inhabiting ponderosa pine/Douglas-fir forests. Because Flammulated Owls in Colorado, Oregon, and Montana nest predominantly in old ponderosa pine/Douglas-fir forests (Bull *et al.* 1990, Goggans 1986, Reynolds and Linkhart 1992), this species may be affected by proposed ponderosa pine ecosystem restoration activities, such as mechanical tree removal and prescribed burning.

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Because old-growth ponderosa pine is rarer in the northern Rocky Mountains than it was historically, and little is known about the local Flammulated Owl distribution and habitat use, the USDA Forest Service has listed the Flammulated Owl as a sensitive species in the Northern Region (USDA 1994). It is also listed as a sensitive species by the USDA Forest Service in the Rocky Mountain, Southwestern, and Intermountain Regions, and receives special management consideration in the States of Montana, Idaho, Oregon, and Washington (Verner 1994).

We conducted a multi-scale analysis of Flammulated Owl habitat use, as part of the USDA Forest Service Bitterroot Ecosystem Management and Research Project (BEMRP) in west-central Montana, USA. BEMRP consisted of an interdisciplinary (wildlife and fisheries biologists, silviculturalists, landscape ecologists, fire ecologists, sociologists) group of researchers and managers, many of whom conducted studies to assess approaches to manage and restore the ponderosa pine ecosystem in the northern Rocky Mountains. Detailed methodology and results of the BEMRP Flammulated Owl habitat use study are reported elsewhere (Wright 1996).

In this paper, we use the results of our multi-scale Flammulated Owl habitat use study and a literature review to address conservation implications of (1) the Flammulated Owl relationship to landscape composition that we observed, and (2) the potential microhabitat (stand-level) effects of proposed ponderosa pine restoration activities on Flammulated Owl habitat.

STUDY AREA

We conducted the BEMRP study of Flammulated Owl habitat use in the low elevation ponderosa pine/Douglas-fir forest zone of the Bitterroot and Sapphire Mountains around the Bitterroot Valley, in west-central Montana (fig. 1). With the exception of a strip of cottonwood (*Populus trichocarpa*) and ponderosa pine forest along the Bitterroot River, the Bitterroot Valley bottom is nonforested. With increasing elevation, the predominantly urban and agricultural lands in the valley bottom grade into grassland (e.g., *Agropyron spicatum, Festuca idahoensis, Festuca scabrella, Balsamorhiza sagittata, Bromis tectorum, Centauria maculosa*) and xeric shrubland (e.g., *Purshia tridentata, Artemesia* spp., *Cercocarpus ledifolius*), and then forested land. Low elevation ridge tops and south-facing slopes in the study area are generally characterized by a mosaic of xeric grassland, xeric shrubland, and relatively low canopy cover ponderosa pine/Douglas-fir forest with a xeric grassland understory, whereas low elevation north-facing slopes and shallow draws contain more contiguous Douglas-fir forest with a moister understory (e.g., *Physocarpus malvaceus, Symphoricarpos albus, Calamagrostis rubescens*). At higher elevations, ponderosa pine/Douglas-fir forests in the study area are replaced by higher canopy cover Douglas-fir forest, or Douglas-fir/western larch (*Larix occidentalis*) forest, with a mesic understory (e.g., *Vaccinium* spp., *Linnaea borealis, Arctostaphylos uva-ursi*). Mesic forests containing lodgepole pine (*Pinus contorta*), subalpine fir (*Abies lasiocarpa*), and Englemann spruce (*Picea engelmanni*) occur above approximately 1,950 m elevation. The highest elevation forest zone is composed of alpine larch (*Larix lyallii*), subalpine fir, and whitebark pine (*Pinus albicaulis*).

Most of the forest in the study area occurs on public land and is managed by the National Forest System (fig. 2). The study area consists of three management zones: (1) unharvested, higher-elevation forest in the Selway-Bitterroot Wilderness area, (2) forest predominantly managed for timber production on National Forest land outside the wilderness, and (3) forest often managed for timber production on private land. Historic timber management outside the wilderness, where most of the ponderosa pine/Douglas-fir forest occurs, has created a variety of even- and uneven-aged harvested forest stands. Even-aged timber management, particularly along the eastern front of the Bitterroot Valley, has created young to mature, single-storied stands of ponderosa pine without large ponderosa pine trees or

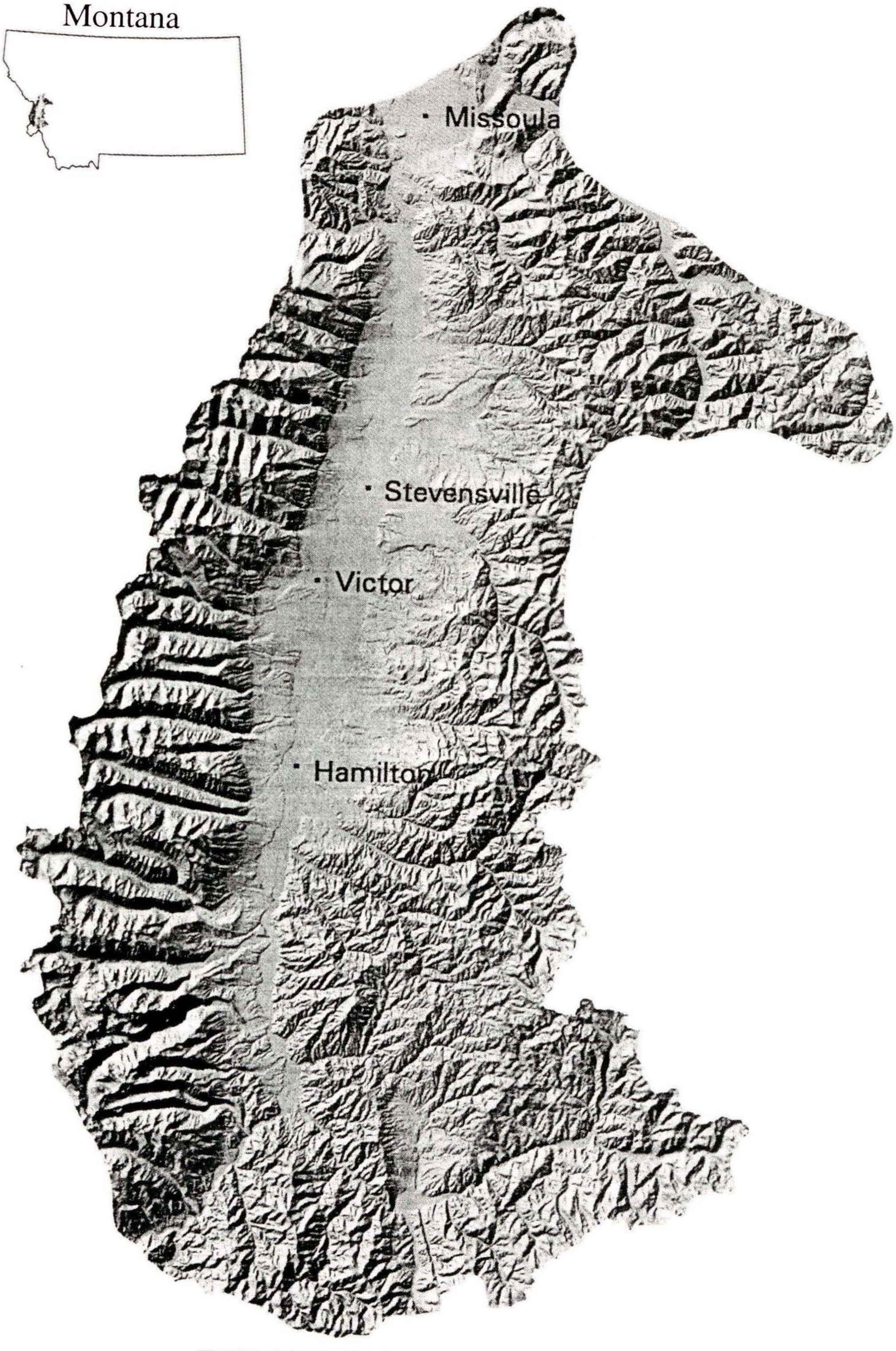
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Figure 1.—*Study area location and topography, west-central Montana, USA.*

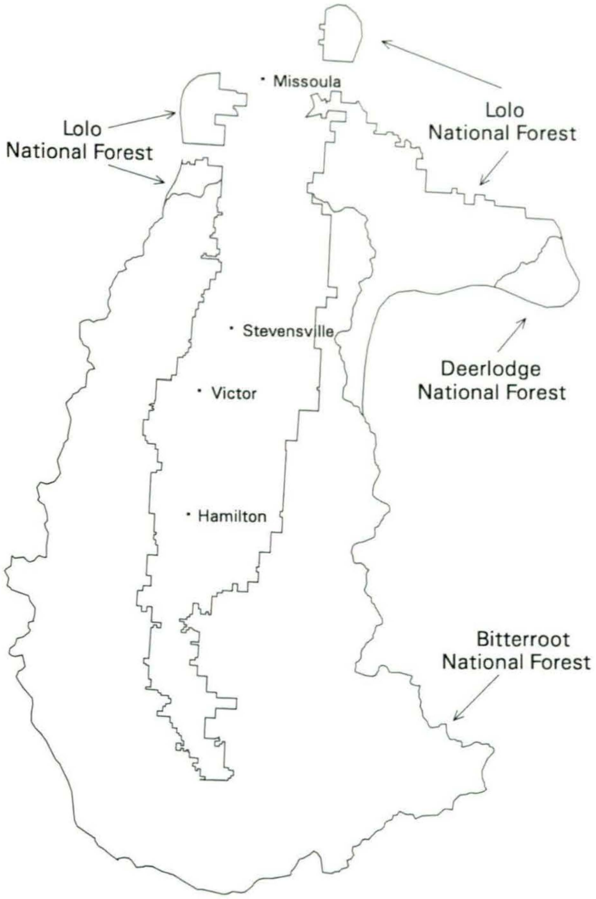

Figure 2.—*Location of National Forest land within the study area, west-central Montana, USA.*

snags. Uneven-aged management has lead to the presence of multi-storied stands throughout the study area, with varying numbers of large ponderosa pine, Douglas-fir trees, and snags.

SUMMARY OF BEMRP FLAMMULATED OWL STUDY

During the multi-scale BEMRP study of Flammulated Owl habitat use, we used tape playback surveys to sample and describe the distribution of Flammulated Owls in a 656,317-ha study area. After describing the owl distribution, we analyzed habitat use at four spatial scales, comparing used and unused habitat by measuring forest stand composition and structural variables within the traditional microhabitat scale of 11.3-m-radius plots, and by quantifying landscape composition at three larger spatial scales: (1) estimated home range around microhabitat plots, (2) surveyed area around transects, and (3) topographically- and geologically-delineated landtype polygons within the study area. For the three landscape scales, we used a vegetative cover-type classification of Landsat TM data with a 2-ha resolution to quantify landscape composition (Redmond *et al.* 1996).

Results of the microhabitat analyses were similar to those reported for previous studies. Flammulated Owls used mature and old-growth ponderosa pine/Douglas-fir forest stands disproportionately more than young ponderosa pine/Douglas-fir or other coniferous forest types. Still, we did not detect owls at 48 percent of the plots that contained these suitable microhabitat cover types. We refer to plots without owl detections as unoccupied. Many of the unoccupied plots had similar stand structure to occupied plots, but occurred in landscapes with a lower proportion of low/moderate canopy closure (< 70 percent cover) ponderosa pine/Douglas-fir forest than landscapes containing occupied plots. When analyses included only plots that occurred in occupied landscapes, those with a relatively high proportion of suitable forest, a greater proportion of suitable microhabitat plots were occupied (fig. 3). Thus, we hypothesize that some points, though suitable at the local scale, might not

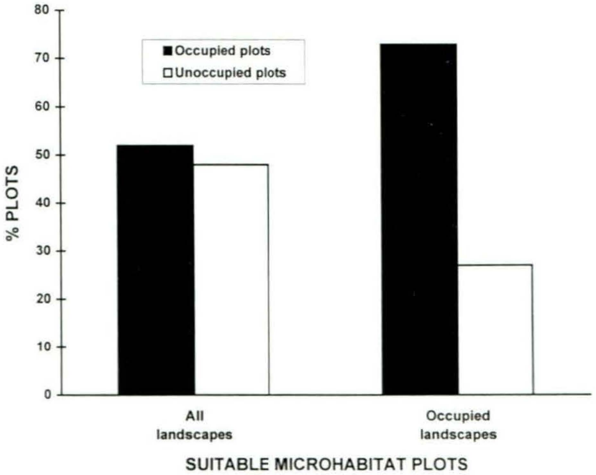

Figure 3.—*Percent of suitable microhabitat (i.e., old-growth and mature ponderosa pine/ Douglas-fir) plots occupied in all landscapes, compared to percent of suitable microhabitat plots occupied only in landscapes occupied by Flammulated Owls (*Otus flammeolus*), west-central Montana, USA.*

have been occupied because they occurred in unsuitable landscapes (Wright 1996). Because Flammulated Owls often occur in association with other Flammulated Owls, this may be related to social requirements, such as mate selection; or, selecting landscapes with an abundance of ponderosa pine/Douglas-fir forest may increase the chance of finding suitable nest sites. Assuming we measured the critical microhabitat attributes, these results help explain why Flammulated Owls are often absent from sites that appear to contain suitable microhabitat, and have patchy distributions.

CONSERVATION IMPLICATIONS

Where to Manage/Conserve Habitat

Within the geographic range of ponderosa pine, managers often identify old-growth ponderosa pine stands as potential Flammulated Owl habitat. These stands are targeted for management actions thought to benefit Flammulated Owls, under the assumption that all old-growth ponderosa pine stands are suitable habitat. Two consequences of this assumption are: (1) if all old-growth ponderosa pine stands are not suitable for Flammulated Owls, there is less habitat available than we think, and (2) habitat conservation and restoration efforts may be wasted if they occur in ponderosa pine forest stands that are not, or do not have the potential to become, suitable habitat.

Flammulated Owls in the BEMRP study area did not occupy all ponderosa pine stand types. Instead, they occupied stands that occurred within landscapes containing a greater proportion of low canopy cover ponderosa pine/ Douglas-fir forest than landscapes around unoccupied stands. Of the occupied landscapes, Flammulated Owl densities were greater in landscapes with more older ponderosa pine/Douglas-fir forest. The mean nearest-neighbor distance we observed (552 m) between owls on transects with an abundance of old forest was three times closer than on transects in landscapes with an abundance of young forest. This is probably because suitable stands were farther apart in landscapes dominated by young forest. Thus, Flammulated Owls in the BEMRP study area used landscapes with an abundance of ponderosa pine/ Douglas-fir forest, and had greater densities in landscapes with an abundance of older ponderosa pine/Douglas-fir forest.

Even within suitable landscapes, all ponderosa pine forest types in the BEMRP study area were not occupied. For instance, we never detected Flammulated Owls in mesic old-growth ponderosa pine stands with a *Vaccinium* understory. Thus, within suitable landscapes, it may be most effective to conserve and restore stand structural characteristics within suitable habitat types (e.g., xeric ponderosa pine/ Douglas-fir stands in our study area), rather than within any stand containing ponderosa pine trees.

While Flammulated Owls in the BEMRP study area appeared to use only suitable forest stands that occurred in suitable landscapes, specific results of the study might have been different if we had defined landscape size differently, conducted the study during a period with different bird densities, or used a vegetative cover-type classification developed with a different unit of resolution. Due to the large number of studies that have found similar associations between Flammulated Owls and microhabitat structural characteristics, microhabitat results may be more broadly extrapolated than the landscape results. Though additional studies should be conducted to confirm specific landscape associations, the BEMRP study supported the idea that landscape context is important when defining suitable habitat for Flammulated Owls.

If the landscape associations identified during the BEMRP study apply elsewhere, querying broad-scale Geographic Information System (GIS) databases for landscapes with an abundance of suitable forest types, may be a useful tool for identifying potentially occupied areas. Identifying landscapes with a high likelihood of occupancy can increase the efficiency of conducting surveys to describe local Flammulated Owl distributions. These queries can also be used to estimate the distribution of currently suitable habitat, recognizing that large areas of ponderosa pine/Douglas-fir forest may be more likely to contain Flammulated Owls than small stands of this forest type.

Geographic Information System queries based on the results of broad-scale studies, such as the BEMRP study described here, can also be used to predict landscapes with past and future Flammulated Owl habitat. For example, areas with an abundance of young ponderosa pine/Douglas-fir forest may represent past habitat that could be managed as potential future habitat. The recruitment of old ponderosa pine/Douglas-fir forest may be most beneficial for Flammulated Owls in areas such as the eastern front of the Bitterroot Mountains, which contain an abundance of ponderosa pine/Douglas-fir forest, but where most of the old-growth ponderosa pine/Douglas-fir forest has been replaced by young, structurally-simple forest stands. BEMRP managers and researchers are currently trying to determine the best method to accomplish this on the Bitterroot National Forest.

Stand Structure

While landscape analyses can help identify suitable landscapes for a species, it is still necessary to maintain suitable microhabitat within suitable landscapes. For example, the regional decline of the Siberian Tit (*Parus cinctus*), a cavity nester of Finland's old-growth forests, was the result of intensive forest management that removed large trees and snags at the microhabitat scale (Virkkala 1991). Similarly, Flammulated Owls that settle in suitable landscapes cannot nest unless there are suitable snags or large trees with nest cavities, as well as other necessary microhabitat features.

Cover Type

Results of the BEMRP study were similar to those reported in previous studies conducted at the microhabitat scale within the geographic and elevational range of ponderosa pine (reviewed in McCallum 1994). Based on vegetation samples taken at the microhabitat scale in our study, Flammulated Owls used old-growth and mature ponderosa pine/Douglas-fir forest more than young ponderosa pine/Douglas-fir or other coniferous forest types. Sample plots near occupied points contained more large (> 38 cm diameter, measured 1.4 m above ground) trees and snags than those near unoccupied points.

Similarly, Flammulated Owls in the northern and central Rocky Mountains (Hayward 1986, Reynolds and Linkhart 1992) and in the Blue Mountains (Bull *et al.* 1990) used predominantly old-growth ponderosa pine forests as nesting and foraging habitat, rather than other old-growth coniferous forest types or young dense stands of Douglas-fir/blue spruce (Reynolds and Linkhart 1987). Occupied habitat in a New Mexico study area (McCallum and Gehlbach 1988) was also located in stands with large ponderosa pine and Douglas-fir or grand fir (> 50 cm d.b.h.) and large-diameter snags with suitable cavities. In a southern British Columbia study area at the extreme northern edge of the Flammulated Owl range, Howie and Ritcey (1987) found Flammulated Owls associated with older open Douglas-fir forests. Regardless of the differences in tree species composition, Howie and Ritcey (1987) agreed with others (Bull 1990, Reynolds and Linkhart 1992) that Flammulated Owls prefer older forests. Atkinson and Atkinson (1990) also found most owls in Douglas-fir habitat types on the Salmon National Forest in Idaho, with structure similar to that described by Howie and Ritcey (1987) in British Columbia.

Large Ponderosa Pine and Douglas-Fir Trees

Large ponderosa pine and Douglas-fir trees are important components of Flammulated Owl habitat for a variety of reasons, including the provision of early-season foraging substrates. Flammulated Owls eat primarily noctuid moths early in the breeding season, and orthopterans later (Goggans 1986, Reynolds and Linkhart 1987). Four times as many lepidopteran species (including noctuids) in a Colorado study area were associated with ponderosa pine and Douglas-fir than with other western conifer species (Reynolds and Linkhart 1987), and most arthropods captured in the Colorado study were in Douglas-fir (61 percent) and ponderosa pine (19 percent) trees with a mean age of 199 years. Early-season prey are most frequently captured by hawk-gleaning inside tree crowns and hover-gleaning from the outer conifer needles (Reynolds and Linkhart 1987). Reynolds and Linkhart (1987) suggested that large open tree crowns, such as those found in large ponderosa pine trees, were used for tree-crown foraging tactics such as hawk-gleaning and hover-gleaning. This is similar to other insectivorous forest bird species that select specific tree species to facilitate maneuvering while foraging (Robinson and Holmes 1984, Vander Werf 1993).

In addition to providing foraging substrates, old ponderosa pine and Douglas-fir trees are often used for song perches and roost sites (Reynolds and Linkhart 1992, Wright 1996), and decadent portions of old trees provide nest sites (see next section). Eighty-two percent of the song trees we observed during the BEMRP habitat-use study were ponderosa pine, possibly because ponderosa pine was often the largest tree species present in occupied stands. Additionally, Flammulated Owls in northeastern Oregon roosted in ponderosa pine more than any other tree species (Goggans 1986).

Flammulated Owls use both large ponderosa pine and Douglas-fir trees within the ponderosa pine/Douglas-fir forest type (Reynolds and Linkhart 1992), and sometimes nest in old-growth Douglas-fir stands (Howie and Ritcey 1987, Powers *et al.* 1996). Thus, where ponderosa pine is absent or rare, large Douglas-fir trees may provide nest, roost, song, and foraging substrates. Because there are fewer ponderosa pine old-growth trees in the northern Rocky Mountains than there were historically, it may be necessary to retain large Douglas-fir, in addition to large ponderosa pine trees, as song trees, foraging trees, and for large snag recruitment. Thus, selective logging that removes large ponderosa pine or Douglas-fir trees would be expected to decrease the availability of early-season feeding sites, song and roost sites, and trees for snag recruitment in areas already limited in large snag abundance. Without studying reproductive success relative to large tree density to gather information on habitat quality, it may be risky to selectively harvest large ponderosa pine or Douglas-fir trees or snags from current habitat.

Selective Tree Harvest

The distribution and abundance of many bird species, including the Flammulated Owl, change with forest habitat alteration. Flammulated Owls do not occur in recently clearcut forests (Howie and Ritcey 1987), and their abundances have declined following this type of timber harvest (Franzreb and Ohmart 1978, Marshall 1957, Phillips *et al.* 1964). However, Flammulated Owls were present in approximately half of the selectively-logged microhabitat plots in the BEMRP study area. Occupied selectively-logged stands contained large residual trees and snags, similar to stands described by Hasenyager *et al.* (1979) and Bloom (1983), who also reported nests in partially logged forests with large residual trees. In a heavily managed study area in British Columbia (Howie and Ritcey 1987), most owls occurred in mature and old stands of Douglas-fir that had been selectively harvested 2-3 decades prior to the surveys. These multi-storied stands contained 35-65 percent overstory canopy closure composed of Douglas-fir and ponderosa pine, a Douglas-fir understory, and a sparse shrub layer. Occupied plots in selectively-logged stands in our study area contained fewer large (> 38 cm diameter) stumps than selectively-logged stands around unoccupied plots, indicating owls used stands that had been harvested less intensively.

The evidence is clear that Flammulated Owls occupy, and sometimes nest in, selectively-logged stands. However, inferences about habitat quality, such as comparing unlogged and selectively-logged sites should be saved for studies that incorporate measures of reproductive success and survivorship. Presence/absence data provide valuable information about which habitats are completely unsuitable; however, it is inappropriate to assume equal habitat quality among all occupied areas (Van Horne 1983). For instance, two forest types may appear suitable based on occupancy data, but reproductive or survivorship data could indicate one type provides higher-quality habitat than another. Thus, our results provide information about which microhabitat and landscape conditions were completely unsuitable in our study area, rather than information about the relative habitat quality of occupied areas.

Large Snags

Flammulated Owls are obligate cavity nesters, dependent on Pileated Woodpeckers (*Dryocopus pileatus*), Northern Flickers (*Colaptes auratus*), and sapsuckers (*Sphyrapicus* spp.) to excavate suitable nest cavities (Bull *et al.* 1990, Powers *et al.* 1996). These woodpecker species excavate cavities in large snags or decadent portions of large live trees. Thus, large snags provide important nesting substrates for Flammulated Owls. Of 33 nests in northeastern Oregon, mean nest tree d.b.h. was 72 cm (Bull *et al.* 1990). Ninety-one percent of the nests found by Bull *et al.* (1990), and 80 percent of 20 nests found by Goggans (1986) were in snags. Additionally, 85 percent of 20 nests in Oregon were in ponderosa pine (Goggans 1986). Most nests observed by Goggans (1986) were ponderosa pine snags, indicating that ponderosa pine snags may be especially important to Flammulated Owls. Thus, selective logging within this forest type that harvests "high-risk" ponderosa pine, trees that are expected to die soon, could remove trees critical to the recruitment of future Flammulated Owl nest trees.

Major Flammulated Owl nest competitors were presumed to be Abert's squirrels (*Sciurus aberti*) and Northern Flickers in New Mexico (McCallum and Gehlbach 1988), and flying squirrels (*Glaucomys sabrinus*) and red squirrels (*Tamiasciurus hudsonicus*) in British Columbia (Cannings and Cannings 1982). Because Flammulated Owls nest later than resident forest owls, they might also be excluded from nest cavities by resident owls such as the Northern Saw-whet (*Aegolius acadicus*) and Northern Pygmy (*Glaucidium gnoma*) Owls. Thus, nest sites may be especially limited if snag densities are low. The abundance of snags and decadent trees was low in our study area, with more than a single large snag evident within 1 ha of only 35 percent of the microhabitat plots. This was probably due to past forest management practices. Managers on the Bitterroot National Forest in the 1950's and 1960's actively removed snags that were thought to be ignition points for lightning strikes, and firewood cutters still often remove large snags. The single unroaded transect in ponderosa pine/Douglas-fir forest in our study area had greater snag densities than roaded transects in this forest type.

Habitat Type

While Flammulated Owls used older ponderosa pine/Douglas-fir stands in the BEMRP study area, they did not use all types of old ponderosa pine/Douglas-fir forest. We assigned habitat type categories to plots based on relative site moisture, as indicated predominantly by understory vegetation composition (Pfister *et al.* 1977). In the BEMRP study, Flammulated Owls occupied stands with dry habitat types. Owls were positively associated with dry-site indicator species such as *Balsamorhizza sagitatta*, and were never found in stands with moist-site plants such as *Salix* spp. and *Vaccinium* spp. The use of xeric ponderosa pine/Douglas-fir forest may be related to food availability; dry openings appear to be important structural elements for Flammulated Owl foraging. These structural elements may limit the types of forest this species inhabits because many coniferous forest types in the northern Rocky Mountains do not contain dry openings.

In a USDA Forest Service summary of habitat types used by Flammulated Owls (J. Taylor, Wildlife Biologist, Idaho Panhandle National Forest) on the Idaho Panhandle, Kootenai, and Payette National Forests in northern Idaho and northwestern Montana, 63 percent of the detections were in xeric ponderosa pine/Douglas-fir habitat types, and 37 percent were in habitat types that were more mesic than sites used in our study area. Douglas-fir, a tree species used by Flammulated Owls, is often the dominant species in seral stands for all the mesic habitat types Flammulated Owls were reported in by the Forest Service summary; however, these habitat types contain moist-site understory plants rather than the xeric grassland understory used by Flammulated Owls in our study area. Owls in those areas might have been solicited through tape playbacks from adjacent xeric stands, or they might use more mesic habitat types in the moister landscapes of northern Idaho and northwestern Montana.

Thus, specific results of our study may not be applicable in regions with different habitats, including areas with aspen or areas without xeric ponderosa pine/Douglas-fir forest. Two types of ponderosa pine forest that existed in our study area were not surveyed during our study. Old-growth ponderosa pine forests occur along many south-facing slopes in the Bitterroot Mountains. These slopes were too steep and rocky to safely traverse at night, and the creek noise from spring runoff was too loud to survey these areas from gentler slopes high above the canyons. The understory vegetation on these slopes was sparse, and may represent lower quality foraging habitat than under the more contiguous ponderosa pine forests that occur on gentler slopes. Additionally, Flammulated Owls in the southeastern region of the study area used home ranges with a lower slope gradient, and it is possible these slopes are too steep to be suitable. Thus, forests on these south-facing slopes represent a different, unsurveyed habitat type that may or may not be suitable. Ponderosa pine also occurred in association with black cottonwood along terraces of the Bitterroot River (Habeck 1990). Based on the presence of cottonwoods, which often have an abundance of cavities, such forests would be expected to contain an abundance of suitable nest trees. Most of these terraces in the study area occur on private land, and many of the large ponderosa pine were removed when the land was settled in the early 1900's (Habeck 1990). Intact examples of this forest type along the Bitterroot River were rare and were not surveyed for Flammulated Owls. Thus, our study results are not applicable to these forest types.

Understory Vegetation

There was no significant difference in the amount of understory Douglas-fir in occupied and unoccupied plots in the BEMRP study in west-central Montana. However, other researchers have noted the importance of understory thickets to Flammulated Owls. For instance, while stands of dense young trees in New Mexico or Oregon (Bull 1990, McCallum and Gehlbach 1988) were not suitable as nest sites, thickets of dense vegetation were present near all nests, and were used for roosting and singing in New Mexico (McCallum and Gehlbach 1988). Reynolds and Linkhart (1992) also observed males singing within dense clumps of foliage, and Flammulated Owls in eastern Oregon predominantly roosted in dense stands with > 50 percent canopy cover. Mean stem density in roost sites observed by Goggans (1986) was 2,016 trees/ha (SD = 1,378, $n = 31$, range 509-5,346), with mean basal area of 129 m^2 (SD = 48.5, $n = 31$, range 21-239). Flammulated Owl use of dense forest thickets was also recorded by Bull and Anderson (1978) and Marcot and Hill (1980).

Because Flammulated Owls use both ponderosa pine and Douglas-fir dominated forest types, the recent floristic change in many ponderosa pine forests to predominantly Douglas-fir might not be expected to affect Flammulated Owl occupancy of stands. However, there are no data on reproductive success in the two forest types. The change in forest structure, from a low canopy cover forest with openings and patchy understory thickets, to a contiguous high canopy forest with fewer openings, might decrease food availability for Flammulated Owls. Densities of orthopteran prey in grassland are greater than in forest, and ponderosa pine/Douglas-fir forests with open canopies have greater food availability than continuous forests (Goggans 1986). For instance, based on insect window trap stations in eastern Oregon, 2.7 times as many prey items occurred in ponderosa pine/Douglas-fir forest, and 8.7 times as many prey items occurred in grassland, than in mixed conifer forest (Goggans 1986). Thus, stands with dense understories probably contain less prey, and hinder foraging maneuverability (Goggans 1986).

While the elimination of some understory forest would be expected to maintain the grassland openings used by foraging owls, management activities that eliminate all understory Douglas-fir may remove thickets important for roosting and singing, for drop-pounce foraging perches, and for predator protection cover. Flammulated Owls roosted an average of 53 m from nests during the nesting period, and < 20 m from nests prior to juvenile fledging; therefore, Goggans (1986) suggested that suitable nest-sites may include patches of dense forest for roosting, as well as openings for foraging.

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LITERATURE CITED

Arno, S.F. 1988. Fire ecology and its management implications in ponderosa pine forests. In: Baumgartner, D.M.; Lotan, J.E., comps. Ponderosa pine: the species and its management; symposium proceedings; 1987 September 29-October 1; Spokane, WA. Pullman, WA: Washington State University, Cooperative Extension: 133-139.

Atkinson, E.C.; Atkinson, M.L. 1990. Distribution and status of Flammulated Owls on the Salmon National Forest. Nongame and Endangered Wildl. Rep. Idaho Department of Fish and Game. 40 p.

Bloom, P.H. 1983. Notes on the distribution and biology of the Flammulated Owl in California. Western Birds. 14: 49-52.

Bull, E.L.; Wright, A.L.; Henjum, M.G. 1990. Nesting habitat of Flammulated Owls in Oregon. Journal of Raptor Research. 24(3): 52-55.

Bull, E.L.; Anderson, R.G. 1978. Notes on Flammulated Owls in northeastern Oregon. Murrelet. 59: 26-28.

Cannings, R.J.; Cannings, S.R. 1982. A Flammulated Owl nest in a nest box. Murrelet. 63: 66-68.

Cody, M.L., ed. 1985. Habitat selection by birds. Orlando, FL: Academic Press, Inc.

Franzreb, K.E.; Ohmart, R.D. 1978. The effects of timber harvesting on breeding birds in a mixed coniferous forest. Condor. 80: 431-441.

Goggans, R. 1986. Habitat use by Flammulated Owls in northeastern Oregon. Corvallis, OR: Oregon State University. M.S. thesis.

Habeck, J.R. 1990. Old-growth ponderosa pine-western larch forests in western Montana: ecology and management. The Northwest Environmental Journal. 6: 271-292.

Hasenyager, R.N.; Pederson, J.C.; Heggen, A.W. 1979. Flammulated Owl nesting in a squirrel box. Western Birds. 10: 224.

Hayward, G. 1986. Activity pattern of a pair of nesting Flammulated Owls (*Otus flammeolus*) in Idaho. Northwest Science. 60(3): 141-144.

Howie, R.R.; Ritcey, R. 1987. Distribution, habitat selection, and densities of Flammulated Owls in British Columbia. In: Nero, R.W.; Clark, R.J.; Knapton, R.J.; Hamre, R.H., eds. Biology and conservation of northern forest owls; symposium proceedings; 1987 February 3-7; Winnipeg, MB. Gen. Tech. Rep. RM-142. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 249-254.

Marcot, B.G.; Hill, R. 1980. Flammulated Owls in northwestern California. Western Birds. 11: 141-149.

Marshall, J.T., Jr. 1957. Birds of the pine-oak woodland of southern Arizona and adjacent Mexico. Pacific Coast Avifauna. 32: 1-125.

McCallum, D.A.; Gehlbach, F.R. 1988. Nest-site preferences of Flammulated Owls in western New Mexico. Condor. 90: 653-661.

McCallum, D.A. 1994. Review of technical knowledge: Flammulated Owls. In: Hayward, G.D.; Verner, J., tech. eds. Flammulated, Boreal, and Great Gray Owls in the United States: a technical conservation assessment. Gen. Tech. Rep. RM-253. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 14-46.

Mutch, R.W.; Arno, S.F.; Brown, J.K.; Carlson, C.E.; Ottmar, R.D.; Peterson, J.L. 1993. Forest health in the Blue Mountains: a management strategy for fire-adapted ecosystems. Gen. Tech. Rep. PNW-310. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 14 p.

Pfister, R.D.; Kovalchik, B.L.; Arno, S.F.; Presby, R.C. 1977. Forest habitat types of Montana. Gen. Tech. Rep. INT-34. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 174 p.

Phillips, A.R.; Marshall, J., Jr.; Monson, G. 1964. The birds of Arizona. Tucson, AZ: University of Arizona Press. 212 p.

Powers, L.R.; Dale, A.; Gaede, P.A.; Rodes, C.; Nelson, L.; Dean, J.J.; May, J.D. 1996. Nesting and food habits of the Flammulated Owl (*Otus flammeolus*) in southcentral Idaho. Journal of Raptor Research. 30(1): 15-20.

Redmond, R.L.; Ma, Z.; Tady, T.P.; Winne, J.C.; Schumacher, J.; Troutwine, J.; Holloway, S.W.; McGuire, C.P.; Righter, R.L.; McWethy, L.G.; Schirokauer, D.W.; Thornton, P.C.; Tobalske, C.; Gustafson, W.; Handley, J.; Hinshaw, J.; Jones, A.;

Stegman, S.; Vander Meer, A.; Hart, M.M.; McLaughlin, K.P.; Williams, W.A. 1996. Mapping existing vegetation and land cover across western Montana and northern Idaho. Final Report. Contract #53-0343-4-000012. Missoula, MT: United States Department of Agriculture, Forest Service, Northern Region.

Reynolds, R.T.; Linkhart, B.D. 1992. Flammulated Owls in ponderosa pine: evidence of preference for old growth. In: Old-growth forests in the southwest and Rocky Mountain Region, proceedings of a workshop. Gen. Tech. Rep. RM-213. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 166-169.

Reynolds, R.T.; Linkhart, B.D. 1990. Extra-pair copulation and extra-range movements in Flammulated Owls. Ornis Scandinavica. 21(1): 74-77.

Reynolds, R.T.; Linkhart, B.D. 1987. The nesting biology of Flammulated Owls in Colorado. In: Nero, R.W.; Clark, R.J.; Knapton, R.J.; Hamre, R.H., eds. Biology and conservation of northern forest owls; symposium proceedings; 1987 February 3-7; Winnipeg, MB. Gen. Tech. Rep. RM-142. Fort Collins, CO: U.S. Department of Agriculture, Forest Service Rocky Mountain Forest and Range Experiment Station: 239-248.

Robinson, S.K.; Holmes, R.T. 1984. Effects of plant species and foliage structure on the foraging behavior of forest birds. Auk. 101: 672-684.

USDA, Forest Service, Northern Region. June 10, 1994. Sensitive species list. Missoula, MT.

Vander Werf, E.A. 1993. Scales of habitat selection by foraging Elepaio in undisturbed and human-altered forests in Hawaii. Condor. 95(4): 980-989.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management. 47(4): 893-901.

Verner, J. 1994. Review of technical knowledge: Flammulated Owls. In: Hayward, G.D.; Verner, J., tech. eds. Flammulated, Boreal, and Great Gray Owls in the United States: a technical conservation assessment. Gen. Tech. Rep. RM-253. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 10-13.

Virkkala, R. 1991. Spatial and temporal variation in bird communities and populations in north-boreal coniferous forests: a multiscale approach. Oikos. 62: 59-66.

Wright, H.A.; Bailey, A.W. 1982. Fire ecology, United States and southern Canada. New York, NY: Wiley.

Wright, V. 1996. Multi-scale analysis of Flammulated Owl habitat use: owl distribution, habitat management, and conservation. Missoula, MT: The University of Montana. 92 p. M.S. thesis.

Poster Papers
and
Other Presentations

Winter Owl Surveying in Central Alberta

Barbara H. Beck and James A. Beck, Jr.[1]

Abstract.—During the past 9 years we have collected data from calling owls at over 400 sites. Most of the calling was done during the winter and almost all of it in central Alberta with much of it in permanently fragmented agricultural/forested areas. We found mainly Great Horned Owls (*Bubo virginianus*) and Northern Saw-whet Owls (*Aegolius acadicus*) with a few Boreal Owls (*Aegolius funereus*), Barred Owls (*Strix varia*), Long-eared Owls (*Asio otus*), Northern Pygmy-owls (*Glaucidium gnoma*) and Great Gray Owls (*Strix nebulosa*). The owls responded to taped calls by giving alarm calls, singing their primary song, and approaching the caller. We have been able to get both Northern Saw-whet Owls and Great Horned Owls to sing their primary song at temperatures as low as -30° C. Our data shows that: (1) Small owls do not seem to be deterred by the calls of larger owls. (2) Owls often respond more readily to calls of other species than to their own. (3) The moon does not appear to affect the response of owls to taped calls. Successful winter calling involves patience, very warm clothing, good equipment and a severe case of cabin fever.

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Increase in Distribution Records of Owl Species in Manitoba Based on a Volunteer Nocturnal Survey Using Boreal Owl (*Aegolius funereus*) and Great Gray Owl (*Strix nebulosa*) Playback

James R. Duncan and Patricia A. Duncan[1]

Abstract.—From 1991 through 1995, extensive owl surveys were conducted in late March and early April in Manitoba. Prior to these surveys, distribution records of owls covered only 16-71 percent of their expected range in Manitoba. The degree to which the survey increased the documented range varied from no increase (6 of 12 species) up to an 88 percent increase for the Northern Saw-whet Owl (*Aegolius acadicus*). The Boreal Owl (*Aegolius funereus*) and Great Gray Owl (*Strix nebulosa*) had the second and third largest increases respectively, a result possibly enhanced by using male territorial call playback for these species. New Northern Hawk Owl (*Surnia ulula*), Barred Owl (*Strix varia*) and Great Horned Owl (*Bubo virginianus*) occurrences were also obtained. This project was initiated under the auspices of the Manitoba Department of Natural Resources.

Nocturnal surveys (spontaneous calling or using playback recordings to elicit calls) have been used to determine the distribution and local status of several owl species (Smith 1987, Takats *et al.* 1997). Such surveys are also used to determine habitat associations (Duncan and Kearns 1997), population densities and fluctuations (Francis and Bradstreet 1997), and to aid in owl nest location (Frith *et al.* 1997). Although generally secretive, owls are extremely vocal during the early breeding season and can be located with relatively little effort using call playback. This technique is based on the territorial behavior of owls; song playback or vocal imitations within a territory will often produce a vocal or visual response by an owl attempting to defend its territory against the "intruder." Because most owls initiate reproduction in early spring, are nocturnal, and occur at low densities, standard breeding bird surveys fail to record long-term population changes for most owl species. Owl prey populations can fluctuate over a period of many years, possibly affecting owl response rates as well. Therefore, to obtain reliable data, surveys need to be conducted over longer periods (Saurola 1997).

In April 1991, under the auspices of the Manitoba Department of Natural Resources, we organized a long-term and extensive owl survey of Manitoba. Our objectives were to:

1. Determine relative owl species distribution and abundance;
2. Determine owl species habitat associations;
3. Describe multi-annual fluctuations in the number of owls detected; and
4. Provide an organized opportunity for volunteers to contribute to our understanding of owl ecology.

This paper assesses the extent to which the survey provided new distribution records. While the primary objective was to survey for all endemic owl species, we initially placed an emphasis on the Boreal Owl (*Aegolius funereus*) and the Great Gray Owl (*Strix nebulosa*) in boreal forest regions. Consequently, only playback of those species were used. Since 1995, the survey has been expanded to include aspen parkland and grassland regions, and here, playback of Northern Saw-whet Owl (*Aegolius acadicus*) and Eastern Screech-owl (*Otus asio*) male territorial calls was used.

METHODS

Survey Technique

In 1991, skilled naturalists were recruited as volunteers. In subsequent years, new volunteers contacted us after they heard or read about the survey. Volunteers were either assigned predetermined routes or were assisted in designing their routes. Route locations were not predetermined randomly or according to any systematic plan. Rather, new routes were generally promoted in areas not currently or previously surveyed. Volunteers were given a map delineating their route, instructions, and data sheets. A cassette tape was provided with recorded calls of 12 owl species (and frog calls) known to occur in Manitoba on one side, and a 20-second call of two target owl species on the other side. Because the survey involved playback, volunteers had to provide a portable tape recorder. The type and loudness of the cassette player was not standardized.

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Surveys, conducted in late March or early April, started 30 minutes after sunset, and finished at least 30 minutes before sunrise. Survey stations were spaced at 0.8 km intervals. Any deviations in station spacings were recorded in the "Remarks" column on the data sheet for that station number, and an overall spacing of 0.8 km between stations was maintained. At each station, there was an initial listening period of 1 minute. All owls detected during this period were recorded. After the initial listening period, a pre-recorded 20-second male Boreal Owl call was played, and owls that were detected in the following 1-minute listening period were recorded. Next, a pre-recorded 20-second male Great Gray Owl call was broadcast, and owls that were detected in the following 1-minute listening period were recorded. The playback call was broadcast even if these species (or any others) had been detected in an earlier listening period. Surveyors recorded if the identification of a sound or owl call was uncertain; these records were not included in our analysis.

Owl Distribution Analysis

Manitoba is a large province, spanning 11 degrees north Latitude (49° to 60° N) and 13 degrees west Longitude (approximately between the meridians of 89° and 102°), with a land area of 65,000,000 ha (Teller 1984). For convenience, the province was divided into 104 rectangles corresponding to one degree Latitude-Longitude grid blocks (hereafter simply "degree blocks"). Survey routes were digitized on a Geographic Information System to determine in which degree block individual owls were detected during the survey. The expected distribution of each owl species was estimated from range maps in Godfrey (1986). Documented owl occurrences in Manitoba were obtained from the Prairie Nest Record Scheme administered by the Manitoba Museum (190 Rupert St., Winnipeg, MB R3B 0N2) and from the Manitoba Avian Records database c/o the Manitoba Naturalists Society (401 - 63 Albert St., Winnipeg, MB R3B 1G4). The estimated range and documented occurrences were mapped and tallied by degree block separately.

RESULTS AND DISCUSSION

A total of 204 volunteers participated from 1991 to 1995 (Duncan and Duncan 1995). The number of routes, and hence the number of km surveyed increased annually, yet the total number of owls detected per km fluctuated considerably (table 1). Prey availability likely influenced the annual number of owls detected per km, at least for such species as the Great Horned Owl (*Bubo virginianus*) (Frank Doyle, unpubl. data in Holroyd and Takats 1997).

Some species (e.g., Great Horned Owl and Short-eared Owl, *Asio flammeus*) are thought to be widely distributed over most of Manitoba; others have a restricted range (table 2). Prior to our survey, the documented distribution of owl species (as estimated by degree block) ranged from 16 to 71 percent of their expected range. The degree to which the survey increased a species' documented range varied from no increase (6 of 12 species) up to an 88 percent increase (table 2). However, five of the six species for which there was no increase may be less detectable by the survey methodology. The Boreal Owl and the Great Gray Owl were the focus of this survey effort. While the survey methodology was not designed to solicit responses from other owl species, all owl responses were recorded, regardless of species. Therefore, there are limitations in assessing non-target owl species' distributions with the methodology used.

A strategy to better assess the distributions of non-target owl species might include a combination of habitat analysis and additional focused survey efforts. Such efforts might include longer time periods spent at survey stations, as this has been found to be important for other owl species (Francis and Bradstreet 1997). Likewise, the breeding season for some owls is slightly later than those targeted in this study, and a survey strategy spanning a different timeframe (e.g., including May) may prove beneficial.

Table 1.—*Summary data from a volunteer-based nocturnal owl survey in Manitoba.*

Year	**Total km surveyed**	**Total number of owls detected**	**Number owls/km**
1991	618	222	0.36
1992	727	152	0.21
1993	807	244	0.30
1994	951	288	0.30
1995	1,532	309	0.20

Table 2.—*Number of one-degree Latitude-Longitude grid blocks (db's) in which an owl species was expected to occur in Manitoba and percent increase in documented range due to nocturnal owl surveys (1991-1995).*

Owl species[1]	**Number of db expected**[2]	**Number of db documented**[3]	**Percent of expected db documented**	**Number of db's including survey data**	**Percent increase in number of db's documented**
NSWO	35	8	23	15	88
BOOW	96	15	16	21	40
GGOW	95	21	22	25	19
NHOW	91	20	22	22	10
BARR	38	13	34	14	8
GHOW	101	31	31	33	6
ESCO	14	10	71	10	0
LEOW	66	19	29	19	0
SEOW	104	22	21	22	0
SNOW	7	18	NA[4]	18	0
BUOW	14	9	64	9	0
BARN	0	3	NA[5]	3	0

[1] NSWO = Northern Saw-whet Owl (*Aegolius acadicus*), BOOW = Boreal Owl (*Aegolius funereus*), GGOW = Great Gray Owl (*Strix nebulosa*), NHOW = Northern Hawk Owl (*Surnia ulula*), BARR = Barred Owl (*Strix varia*), GHOW = Great Horned Owl (*Bubo virginianus*), ESCO = Eastern Screech-owl (*Otus asio*), LEOW = Long-eared Owl (*Asio otus*), SEOW = Short-eared Owl (*Asio flammeus*), SNOW = Snowy Owl (*Nyctea scandiaca*), BUOW = Burrowing Owl (*Speotyto cunicularia*), and BARN = Barn Owl (*Tyto alba*).

[2] Based on Godfrey (1986).

[3] Data from the Prairie Nest Record Scheme, Manitoba Museum and Manitoba Avian Records, Manitoba Naturalists Society, Winnipeg, MB.

[4] The Snowy Owl breeds in extreme northern Manitoba, whereas the majority of documented occurrences are during winter in southern Manitoba.

[5] Manitoba is outside the normal breeding range of the Barn Owl.

Owl Species with no Increase in Documented Distribution

Although Manitoba is north of the usual breeding range of the Barn Owl (*Tyto alba*) (Godfrey 1986) there is one documented breeding record (the nest with eggs was unsuccessful) and other records are considered to be casual occurrences (Nero 1995). The Snowy Owl (*Nyctea scandiaca*) nests sporadically in extreme northern Manitoba (Godfrey 1986), an area that has yet to be included in this survey. Nonetheless, some late migrant Snowy Owls were observed in southern Manitoba during the survey period by survey volunteers.

The Burrowing Owl (*Speotyto cunicularia*), Long-eared Owl (*Asio otus*) and Short-eared Owl are migratory in Manitoba, although a few individuals of the latter two species occasionally overwinter in southern parts of the province (Godfrey 1986). The timing of the survey (late March to mid-April) may be less optimal for detecting these species, especially in years with thick snow cover and late snow melt. In addition, the Burrowing Owl was increasingly rare over the survey period in Manitoba (DeSmet 1997).

The Eastern Screech-owl occurs in southern Manitoba and is mainly restricted to riparian areas near adequate prey populations (Walley and Clyde 1996, table 2). A detailed examination of the survey data reveals new documented occurrences for this species (Duncan and Duncan, unpubl. data); these were masked by the coarse scale of the degree blocks used to estimate species' distributions in this analysis.

Owl Species with an Increase in Documented Distribution

The Boreal Owl and Great Gray Owl had relatively large increases in their documented range as a result of the survey (table 2). We speculate that this is due, in part, to the targeted use of playback of male territorial calls for these species during the surveys. Francis and Bradstreet (1997) documented an improved response rate for the Boreal Owl, and possibly for the Great Gray Owl, with playback in surveys in Ontario. Interestingly, the largest increase was for the Northern Saw-whet Owl, a species thought to be an aggressive competitor of the congeneric Boreal Owl (Lane 1988). This result may relate to the idea that some owls often respond more readily to the playback calls of other owl species than to their own (Beck and Beck in Holroyd and Takats 1997). New occurrences of the Northern Hawk Owl (*Surnia ulula*), Barred Owl (*Strix varia*) and Great Horned Owl were also documented during the survey (table 2).

CONCLUSIONS

Volunteer-based nocturnal surveys can effectively document new occurrences of owl species. With a strategic plan to survey areas with little or no information on target species, information can be obtained to better determine a species' distribution, and hence conservation status, in a province or state. More importantly, from a conservation perspective, volunteer-based nocturnal owl surveys give participants an opportunity to explore a different world where senses other than sight play an important role. In addition to increasing data on owl distribution, a host of volunteers have gained a greater appreciation for owls and their habitats.

"The dancing apparitions ahead of us turned out to be nothing more than the car's lights, reflecting off puddles into the mist rising out of the weed-choked ditch. Laughing nervously, we attributed our sudden case of 'the chills' to the cold and damp night air. Still, I was eternally grateful for my partner's presence as we left the vehicle and stepped into the darkness ...." Anonymous Owl Surveyor, 1991.

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François Blouin kindly digitized owl survey routes on a Geographic Information System. We are grateful to Herb Copland for his help in obtaining access to the Prairie Nest Record Scheme administered by the Manitoba Museum. Brian Knudsen assisted by preparing a list of owl records from the Manitoba Avian Records database c/o the Manitoba Naturalists' Society. Robert Nero, David Johnson, and Kurt Mazur constructively reviewed early drafts of the manuscript.

LITERATURE CITED

De Smet, K. 1997. Burrowing Owl (*Speotyto cunicularia*) Monitoring and Management Activities in Manitoba, 1987-1996. In: Duncan, J.R.; Johnson, D.H.; Nicholls, T.H., eds. Biology and conservation of owls of the northern hemisphere: 2d International symposium; 1997 February 5-9; Winnipeg, MB. Gen. Tech. Rep. NC-190. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station: 123-130.

Duncan, J.R.; Duncan, P.A. 1995. Manitoba's nocturnal owl survey: 1995 progress report. Balmoral, MB: Unpublished Report. 6 p.

Duncan, J.R.; Kearns, A.E. 1997. Habitat Associated with Barred Owl (*Strix varia*) Locations in Southeastern Manitoba: A Review of a Habitat Model. In: Duncan, J.R.; Johnson, D.H.; Nicholls, T.H., eds. Biology and conservation of owls of the northern hemisphere: 2d International symposium; 1997 February 5-9; Winnipeg, MB. Gen. Tech. Rep. NC-190. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station: 138-147.

Francis, C.M.; Bradstreet, M.S.W. 1997. Monitoring boreal forest owls in Ontario using tape playback surveys with volunteers. In: Duncan, J.R.; Johnson, D.H.; Nicholls, T.H., eds. Biology and conservation of owls of the northern hemisphere: 2d International symposium; 1997 February 5-9; Winnipeg, MB. Gen. Tech. Rep. NC-190. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station: 175-184.

Frith, S.D.; Mazur, K.M.; James, P.C. 1997. A Method for Locating Barred Owl (*Strix varia*) Nests in the Southern Boreal Forest of Saskatchewan. In: Duncan, J.R.; Johnson, D.H.; Nicholls, T.H., eds. Biology and conservation of owls of the northern hemisphere: 2d International symposium; 1997 February 5-9; Winnipeg, MB. Gen. Tech. Rep. NC-190. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station: 545-547.

Godfrey, W.E. 1986. The birds of Canada. (rev. ed.) Ottawa, ON: National Museums of Natural Sciences. 595 p.

Holroyd, G.L.; Takats, D.L. 1997. Report on the nocturnal raptor monitoring workshop. In: Duncan, J.R.; Johnson, D.H.; Nicholls, T.H., eds. Biology and conservation of owls of the northern hemisphere: 2d International symposium; 1997 February 5-9; Winnipeg, MB. Gen. Tech. Rep. NC-190. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station: 610-612.

Lane, B. 1988. 1988 Boreal Owl survey in Cook County. Loon. 60: 99-104.

Nero, R.W. 1995. Barn Owl nesting in Manitoba. Blue Jay. 53: 159-166.

Saurola, P.L. 1997. Monitoring Finnish Owls 1982–1996: Methods and Results. In: Duncan, J.R.; Johnson, D.H.; Nicholls, T.H., eds. Biology and conservation of owls of the northern hemisphere: 2d International symposium; 1997 February 5-9; Winnipeg, MB. Gen. Tech. Rep. NC-190. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station: 363-380.

Smith, D.G. 1987. Owl census techniques. In: Nero, R.W.; Clark, R.J.; Knapton, R.J.; Hamre, R.H., eds. Biology and conservation of northern forest owls: symposium proceedings; 1997 February 3-7; Winnipeg, MB. Gen. Tech. Rep. RM-142. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 304-309.

Takats, D.L.; Holroyd, G.L. 1997. Owl broadcast surveys in the Foothills Model Forest, Alberta, Canada. In: Duncan, J.R.; Johnson, D.H.; Nicholls, T.H., eds. Biology and conservation of owls of the northern hemisphere: 2d International symposium; 1997 February 5-9; Winnipeg, MB. Gen. Tech. Rep. NC-190. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station: 421-431.

Teller, J.T. 1984. Natural heritage of Manitoba: legacy of the ice age. Winnipeg, MB: Manitoba Museum of Man and Nature, and Manitoba Nature Magazine. 208 p.

Walley, W.J.; Clyde, C.F. 1996. Occurrence and breeding of the Eastern Screech-owl north of the Riding Mountains, Manitoba. Blue Jay. 54: 89-100.

Intra- and Interspecific Calling in a Tropical Owl Community

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Abstract.—We studied the intra- and interspecific responses to playback of pre-recorded calls by five tropical humid forest owl species at La Selva preserve in northeastern Costa Rica from April to September 1995. Response to conspecific broadcast calls differed among species ($X^2 = 24.4$; df = 1; $P < 0.001$): Vermiculated Screech-owls (*Otus guatemalae*) responded to 47.6 percent of broadcasts, followed by Crested Owls (*Lophostrix cristata*, 45 percent), Mottled Owls (*Ciccaba virgata*, 18.3 percent), and Black-and-white Owls (*C. nigrolineata*, 9 percent). Crested Owls ($\bar{x} = 16.37$, sd = 2.6), Mottled Owls ($\overline{x} = 11.7$, sd = 7.1), and Vermiculated Screech-owls ($\overline{x} = 10.9$, sd = 0.9) responded to interspecific playback more than did Black-and-white Owls ($\overline{x} = 2.04$, sd = 2) (H = 10.6; P = 0.01). Spectacled Owls (*Pulsatrix perspicilata*) did not respond at all during our broadcasting period. Both types of response showed some monthly variation. Response to the calling of other owls also depended on ecological variables such as habitat selection, population density, and resource use. Our data suggest that the development of relationships within the tropical owl community at La Selva may have been mediated in part by intra- and interspecific calling.

The interactions between owl species in tropical communities have been poorly studied. In northern Europe, the behavioral ecology of owl communities has received some attention (Korpimäki 1987), but no community-based owl research has been conducted in the Neotropics. Single-species research has examined the food habits (Gerhardt *et al.* 1994a) and breeding biology (Gerhardt *et al.* 1994b) of Neotropical owls, and the calling behavior of one widespread species (Gerhardt 1991). Community ecology is central to understand factors that regulate the structure, dynamics, and evolution of owl populations (Pianka 1988), and the effects of an inter- and intra-species interaction, and eventually, the conservation of those communities. In this paper we report the calling interactions among five Neotropical rainforest owls from La Selva Biological Station, Costa Rica.

STUDY AREA

La Selva Biological Station is located in Sarapiquí county, Heredia province, Costa Rica (10°26'N 83°59'W). The station adjoins Braulio Carrillo National Park to the south and agricultural land and cattle pasture to the north. La Selva encompasses 1,513 ha, and main habitats are primary humid forest, young second growth, grassland in the process of succession, abandoned plantations, swamps, forest study plots, and open areas with buildings. Elevation ranges from 35 to 150 m. Weather conditions are very humid, with 4,000 to 4,500 mm of annual precipitation. Annual temperatures range from 24.7 to 27.1°C.

METHODS

Intra- and interspecific interactions among five owl species; Vermiculated Screech-owl (*Otus guatemalae*), Crested Owl (*Lophostrix cristata*), Spectacled Owl (*Pulsatrix perspicilata*), Mottled Owl (*Ciccaba virgata*), and Black-and-white Owl (*C. nigrolineata*), were studied through broadcasting of vocalizations from April to September 1995. Broadcasting has been a consistent method for surveying woodland owls in North America (Ganey 1990, McGarigal and Fraser 1985, Mosher *et al.* 1990), and the Neotropics (Enríquez 1995, Gerhardt 1991).

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At La Selva, and prior to our broadcasting period, we recorded the typical vocalizations of the five owl species studied. An Uher 4000RL and an Electrovoice Unidirectional Microphone were used to record the vocalizations. Once we had obtained quality recordings, they were copied onto independent cassettes for each owl species. Closed loop cassettes used consisted of 3 minutes of typical vocalizations; "hoot" rates differed slightly among species.

We established 30 survey stations on three major trails (10 stations/trail). The trails selected covered proportionally all habitats at La Selva ($P > 0.05$, Enríquez 1995). Starting points at each trail were at least 400 m apart. Survey stations along trails were 200 m apart from each other following Forsman (1983). The sampling period was 10 minutes at each station, consisting of 3 minutes of broadcasting followed by 7 minutes of listening. Throughout this period, we noted the vocalizations of any owl that responded. To avoid provoking different species at the same station (Kochert 1986), we randomly selected the broadcast order of the five species and played the vocalizations of only one species at each station. Then, we selected a new broadcast order twice on each trail. We conducted surveys on each trail twice monthly ($N = 36$). No surveys were conducted during rain. Sampling methods are described in more detail in Enríquez (1995). Collected data were analyzed using a Chi-square test (X^2) to evaluate the intraspecifc response, a Kruskal-Wallis test (H) to compare multiple intra- and interspecific response percentages, Kolmogorov-Smirnov two sample test (D) for testing distributions of species responses to coexisting species and responses of coexisting species to the target species, and Shapiro-Wilk statistic (W) to test that interspecific responses followed a normal distribution.

RESULTS

The owl community in La Selva and the surrounding area are represented by eight species; five are listed in table 1 and, the Barn Owl (*Tyto alba*), Least Pygmy-owl (*Glaucidium minutissimum*), and Striped Owl (*Asio clamator*). During our broadcasting period we taped 340 broadcast vocalizations. An intraspecific response was obtained 82 times (25 percent of total broadcasts), whereas an interspecific response was obtained 110 times (32.3 percent). The Spectacled Owl did not respond at all during our broadcasting period.

Intraspecific Responses

Most of the owl species at La Selva responded generally more to the broadcasting of conspecific vocalizations (table 1). Percentages of intraspecific responses differed among owl species ($X^2 = 24.4$, df 1, $P < 0.001$). The Vermiculated Screech-owl and Crested Owls had higher percentages of intraspecific responses than Mottled and Black-and-white Owls (table 1).

Among those owl species that responded intraspecifically, variation on monthly percent

Table 1.—*Total mean of response percentages to broadcasting of pre-recorded vocalizations of five species of tropical humid forest owls at La Selva preserve in northeastern Costa Rica, from April to September, 1995.*

	Broadcasting Vocalization by[1]				
Responses by[1]	**VSO**	**CO**	**SO**	**MO**	**BWO**
VSO	47.62	11.51	10.10	11.36	10.67
CO	16.89	45.11	16.63	18.55	13.42
SO					
MO	7.19	6.95	15.10	18.29	17.63
BWO		3.05	5.11		9.01

[1] VSO (Vermiculated Screech-owl), CO (Crested Owl), SO (Spectacled Owl), MO (Mottled Owl), BWO (Black-and-white Owl).

of responses was distributed normally (Shapiro-Wilks test, $P > 0.05$). Crested and Vermiculated Screech-owls showed more monthly variation in intraspecific response than did Mottled and Black-and-white Owls ($H = 15.05$, df 3, $P < 0.05$) (fig. 1).

Interspecific Responses

Species that responded to calls of all other sympatric species included in this survey were Crested Owl, Vermiculated Screech-owl, and Mottled Owl. Meanwhile, the Black-and-white Owl responded to only two sympatric species the Crested Owl and the Spectacled Owl (table 1). Crested Owls responded more frequently to interspecific broadcast vocalizations ($\bar{x} = 16.37$, sd = 2.6) than did Mottled Owls ($\bar{x} = 11.7$, sd = 7.1), Vermiculated Screech-owls ($\bar{x} = 10.9$, sd = 0.9), or Black-and-white Owls ($\bar{x} = 2.04$, sd = 2) ($H = 10.6$; $P < 0.01$). On the other hand, we did not find differences in response to any one of the five owl vocalizations broadcast ($H = 2.06$; $P = 0.72$).

Crested Owls responded more frequently to other species than other species responded to Crested Owls' broadcast vocalizations ($D = 1.41$, $P < 0.05$). We did not find this behavior for any other owl species surveyed ($P > 0.05$). Monthly variation of interspecific responses is shown in figures 2-5. Vermiculated Screech-owls showed some monthly variation in response to Black-and-white Owl vocalizations ($W = 0.659$, $P < 0.05$) (fig. 3). Also, Black-and-white Owls exhibited monthly variation in their response to vocalizations of Crested Owls ($W = 0.678$, $P < 0.05$) and Spectacled Owls ($W = 0.7$, $P < 0.05$) (fig. 5).

DISCUSSION

Responses to broadcast of conspecific calls were more frequent than interspecific responses at La Selva for two of five species studied. Our results suggest that Crested, Vermiculated Screech-, and Mottled Owls were more responsive, both intra- and interspecifically, than Black-and-white and Spectacled Owls. In temperate forest, interspecific responses also varied among owl species, mostly during the breeding season (Bosakowski *et al.* 1987, Springer 1978). But, Smith *et al.* (1987) found that the Eastern Screech-owl (*Otus asio*)

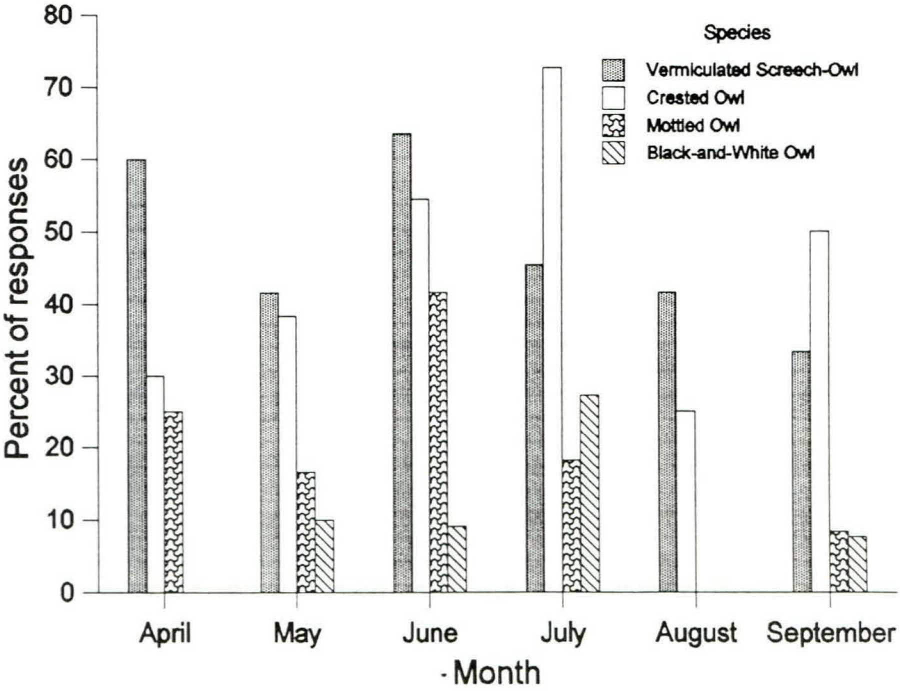

Figure 1.—*Monthly responses to intraspecific broadcasting of pre-recorded vocalizations of four species of tropical humid forest owls at La Selva preserve, northeastern Costa Rica, in 1995.*

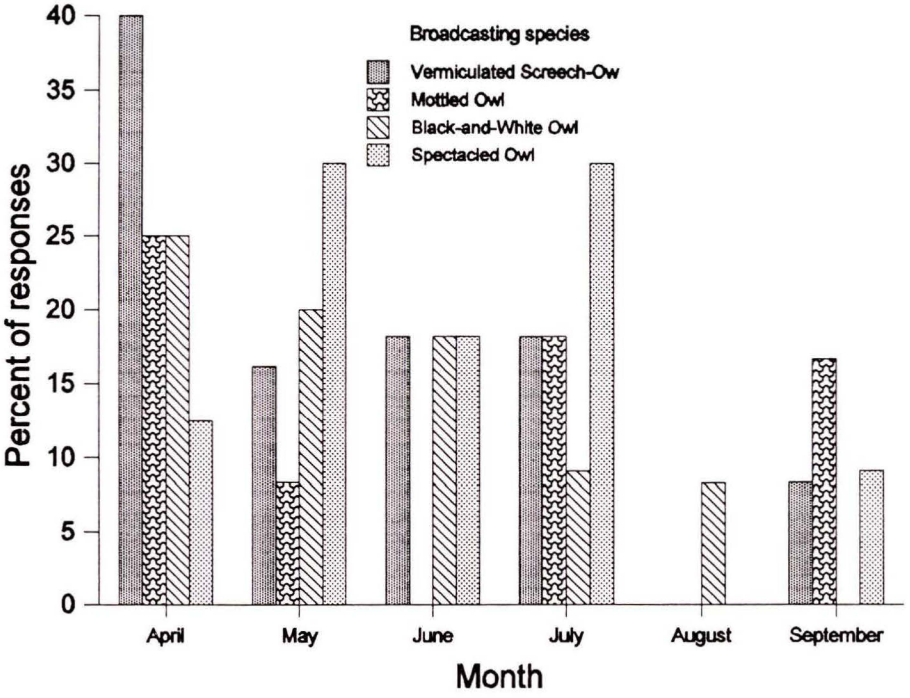

Figure 2.—*Crested Owl monthly responses to interspecific broadcasting vocalizations of co-existing species of tropical humid forest owls at La Selva preserve, northeastern Costa Rica, in 1995.*

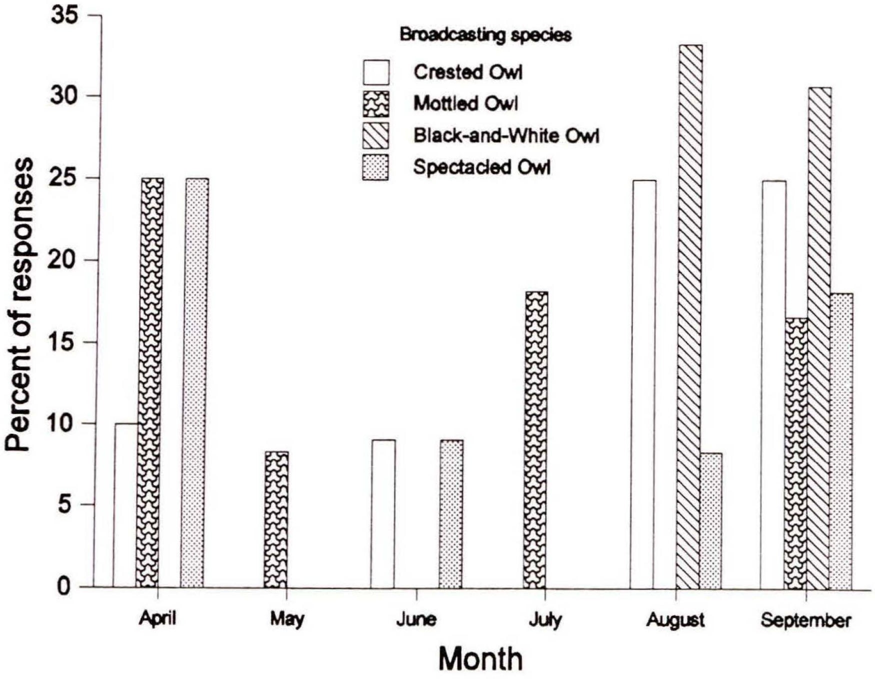

Figure 3.—*Vermiculated Screech-owl monthly responses to interspecific broadcasting vocalizations of co-existing species of tropical humid forest owls at La Selva preserve, northeastern Costa Rica, in 1995.*

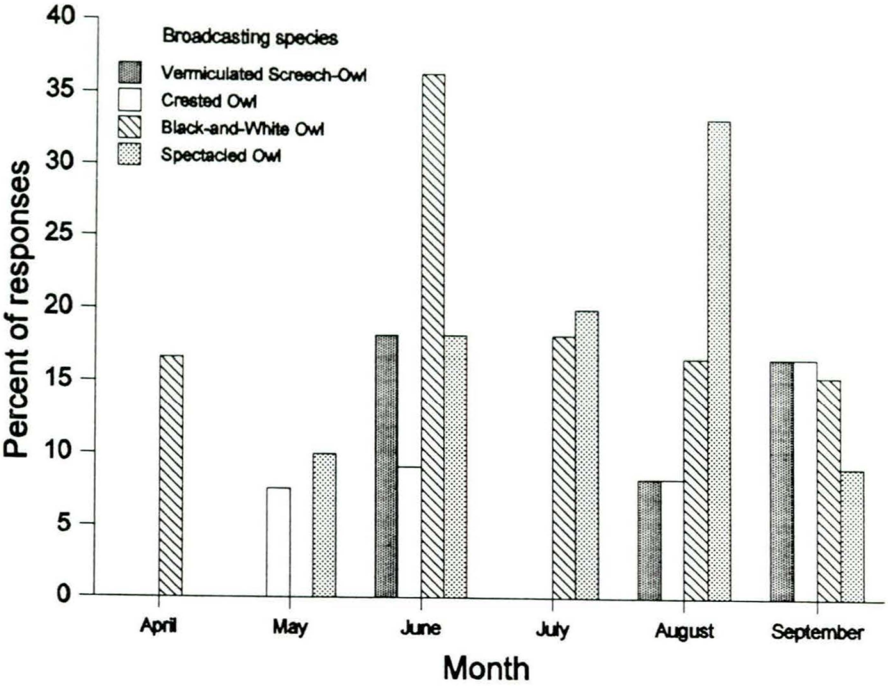

Figure 4.—*Mottled Owl monthly responses to interspecific broadcasting vocalizations of co-existing species of tropical humid forest owls at La Selva preserve, northeastern Costa Rica, in 1995.*

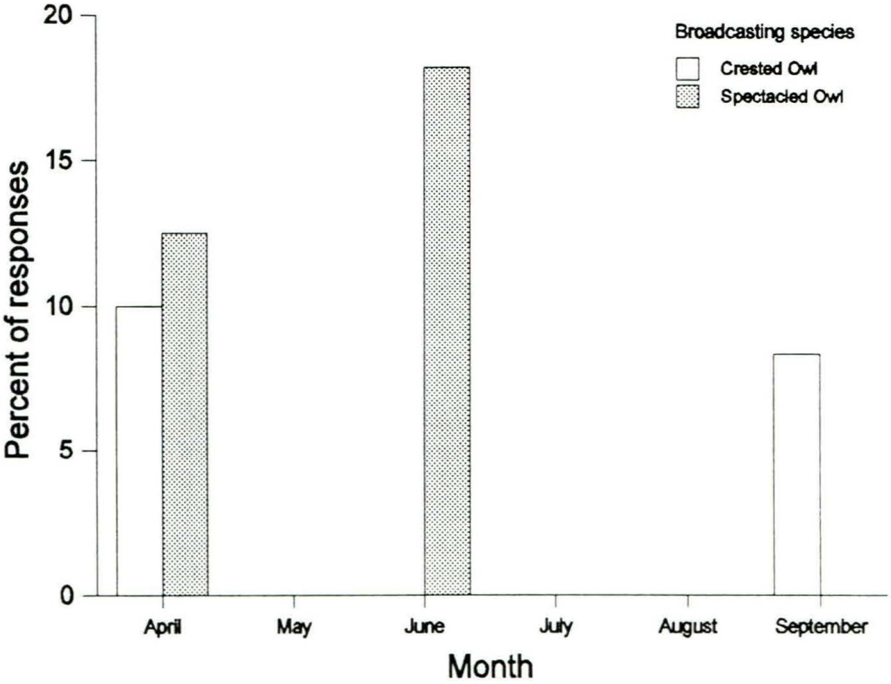

Figure 5.—*Black-and-white Owl monthly responses to interspecific broadcasting vocalizations of co-existing species of tropical humid forest owls at La Selva preserve, northeastern Costa Rica, in 1995.*

responded less during the breeding season. In a tropical forest in Guatemala, Gerhardt (1991) reported that Mottled Owls responded to 40 percent of broadcasts during the breeding season. Mottled Owls responded less frequently in our study site than they did in Guatemala. Crested and Vermiculated Screech-owls responded to over 45 percent of conspecific broadcasts. The differences in the percentage of responses to broadcasting could be related in part to the species abundance in the study area. Enríquez (1995) found that Crested and Vermiculated Screech-owls were quite abundant and Spectacled Owls less abundant at La Selva. Lack of responses by Spectacled Owls and few responses by Black-and-white Owls could be associated with their home range size. In Guatemala, a single Black-and-white Owl had a home range 20 times larger than Mottled Owls had (Gerhardt *et al.* 1994b).

Habitat influences the abundance of some species (Will 1986). Forests and old second growth habitats at La Selva favor the Crested Owl. This rare species is probably a relict of a group that spread around the tropics and survived in old forests with small changes through the period of climatic cooling (Hekstra 1973). The Vermiculated Screech-owl and Mottled Owl are widely distributed and common in Neotropical forests (Gerhardt 1991, Stiles and Skutch 1989). On the other hand, Spectacled Owls use open habitats with nearby woodlots to vocalize, hunt, roost, and breed. The Black-and-white Owl is rare throughout its entire distribution and may not use a particular habitat at La Selva (Enríquez 1995). We recorded this species in different habitats, calling and probably hunting. Nicholls and Warner (1972) mentioned that although owl species may use one habitat more than another, the habitat that is used less may not be less important, since it could contain resources critical to the species' survival.

We did not find seasonality in owl responses in this study; Spectacled Owls, however, vocalized from January to March only. Therefore this species had a seasonality to its calling behavior and our surveys were conducted outside the season during which it was most vocal.

Interspecific relations may include overlap in distribution, hunting period, habitats, and food (Mikkola 1983). Three species (Crested Owl, Vermiculated Screech-owl, and Mottled Owl) at La Selva responded to all other species included in this survey. Meanwhile, Black-and-white Owls responded to only two owl species. Crested Owls responded more frequently to interspecific broadcast vocalizations than did Mottled Owls, Vermiculated Screech-owls, and Black-and-white Owls. The observed differences in interspecific responses at La Selva may be related to differences in population density, habitat use, and food habits. Also, calling behavior of forest owls is affected by environmental variables (Carpenter 1987), as observed at La Selva (Enríquez 1995).

Crested Owls responded more to Mottled Owl vocalizations than other species pair combinations. These species used the same habitat at La Selva (Enríquez 1995). We found these species calling together in different vegetation strata. Mottled Owls feed on vertebrates like small rodents, but are considered mainly insectivorous (Gerhardt *et al.* 1994a). Possibly these species differ in feeding time, strategies and sites. On the other hand, the Mottled Owl is more tolerant of habitat change and so is both abundant and broadly distributed (Mikkola 1992). Also, Mottled Owls can visit urban areas to feed.

Ciccaba owls showed also a high level of interaction, mostly when Mottled Owls responded to Black-and-white Owl calls. These *Ciccaba* species overlapped in distribution and activity patterns, and several times we listened to both species calling simultaneously. Although these species both took large numbers of insects, the mammalian part of their diet showed little overlap (Gerhardt *et al.* 1994a), they likely used different foraging strategies and capture techniques, and they used quite different breeding sites (Gerhardt *et al.* 1994b).

In order of size, Vermiculated, Mottled, and Crested Owls feed mainly on invertebrates (Hekstra 1973), Black-and-white and Spectacled Owls feed mainly on vertebrates (Ibañez *et al.* 1992). Insects, caterpillars, crabs, mammals, birds, and reptiles were reported as prey for Spectacled Owl (Mikkola 1992). Johnsgard (1988) mentioned that owl species that feed mainly on insects have small territories. For those owl species that have similar diets, competition can be reduced by utilizing different time or space. For Crested and Vermiculated Screech-owls, the habitat most utilized was the cacao orchard, but these species occupied different vegetation strata. We found

Crested Owls calling in the canopy and Vermiculated Screech-owls were in the understory. Crested Owls roost in the mid-canopy of the forest and Vermiculated Screech-owls in dense shrubs.

At La Selva forest preserve, the Crested Owl, Vermiculated Screech-owl, and Mottled Owl responded more to intra- and interspecific broadcasting vocalizations; Black-and-white Owls responded less, and Spectacled Owls not at all. Differences in response levels to other owl species depended on ecological variables such as habitat selection, population density, and resource used. Our data suggest that the development of relationships within the tropical owl community at La Selva may have been mediated in part by intra- and interspecific calling behavior. The interspecific relationships could be a mechanism of habitat and resource selection, and knowledge or these interactions would be useful in developing management plans or conservation programs (Mikkola 1983). Habitat transformation in the surrounding area at La Selva has shown that owl abundances have varied through time (Enríquez 1995). In the Neotropics, protected areas such as reserves and national parks function as refuges for many species of wildlife that depend on forested habitats (e.g., Crested Owls). Finally, further information on owl behavior is required in order to better understand the ecology of owl communities and factors affecting owls in protected natural areas. Indeed, in tropical areas habitat is the most important factor to protect and to safeguard an owl community (Mikkola 1983).

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LITERATURE CITED

Bosakowski, Thomas; Spelser, R.; Benzinger, J. 1987. Distribution, density, and habitat relationships of the Barred Owl in North New Jersey. In: Nero, R.W.; Clark, R.J.; Knapton, R.J.; Hamre, R.H., eds. Biology and conservation of northern forest owls: symposium proceedings; 1987 February 3-7; Winnipeg, MB. Gen. Tech. Rep. RM-142. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 135-143.

Carpenter, W. Thomas. 1987. Effect of environmental variables on responses of Eastern Screech-owl to playback. In: Nero, R.W.; Clark, R.J.; Knapton, R.J.; Hamre, R.H., eds. Biology and conservation of northern forest owls: symposium proceedings; 1987 February 3-7; Winnipeg, MB. Gen. Tech. Rep. RM-142. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 277-280.

Enríquez, Paula L. 1995. Abundancia relativa, uso de hábitat y conocimiento popular de los Strigiformes en un bosque húmedo tropical en Costa Rica. Heredia, Costa Rica: Universidad Nacional. 81 p. M.S. dissertation.

Forsman, Eric D. 1983. Methods and materials for locating and studying Spotted Owls. Gen. Tech. Rep. PNW-162. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 8 p.

Ganey, Joseph. 1990. Calling behavior of Spotted Owls in Northern Arizona. Condor. 92: 485-490.

Gerhardt, Richard. 1991. Response of the Mottled Owl (*Ciccaba virgata*) to broadcast of conspecific call. Journal of Field Ornithology. 62(2): 239-244.

Gerhardt, Richard; Gerhardt, D.M.; Flatten, C.J.; Bonilla, G.N. 1994a. The food habits of sympatric *Ciccaba* owls in Northern Guatemala. Journal of Field Ornithology. 65(2): 258-264.

Gerhardt, Richard; Bonilla, G.N.; Gerhardt, D. M.; Flatten, C.J. 1994b. Breeding biology and home range of two *Ciccaba* owls. Wilson Bulletin. 106(4): 629-639.

Hekstra, G.P. 1973. Scops and screech owls. In: Owls of the world. London, England: Peter Lowe, Eurobook: 94-115.

Ibañez, C.; Ramo, C.; Busto, B. 1992. Notes on food habits of the Black-and-white Owl. Condor. 94: 529-531.

Johnsgard, Paul. 1988. North American owls. Washington, DC: Smithsonian Institution Press. 295 p.

Kochert, M.N. 1986. Raptors. In: Inventory and monitoring of wildlife habitat. U.S. Department of the Interior: 313-349.

Korpimäki, Erkki. 1987. Composition of the owl communities in four areas in western Finland: importance of habitats and interspecific competition. In: Proceedings of the 5th Nordic ornithological congress; 1985; Acta Regiae Societatis Scientiarum et Litterarum Gothoburgensis Zoologica. 14: 118-123.

McGarigal, K.; Fraser, J.D. 1985. Barred Owl responses to recorded vocalizations. Condor. 87: 552-553.

Mikkola, Heimo. 1983. Owls of Europe. Calton, England: T. & A.D. Poyser. 397 p.

Mikkola, Heimo. 1992. Wood owls. In: Owls of the world. Netherlands, Holland: Peter Lowe, Eurobook: 108-140.

Mosher, James, A.; Fuller, M.R.; Kopeny, M. 1990. Surveying woodland raptors by broadcast of conspecific vocalizations. Journal of Field Ornithology. 61(4): 453-561.

Nicholls, Thomas H.; Warner, D.W. 1972. Barred Owl habitat use as determined by radiotelemetry. Journal of Wildlife Management. 36: 213-225.

Pianka, Eric. 1988. Evolutionary ecology. New York, NY: Harper & Row. Publishers. 468 p.

Smith, Dwight; Devine, A.; Walsh, D. 1987. Censusing Screech Owls in southern Connecticut. In: Nero, R.W.; Clark, R.J.; Knapton, R.J.; Hamre, R.H., eds. Biology and conservation of northern forest owls: symposium proceedings; 1987 February 3-7; Winnipeg, MB. Gen. Tech. Rep. RM-142. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 255-267.

Springer, M.A. 1978. Foot surveys versus owl calling surveys: a comparative study of two Great Horned Owl censusing techniques. Inland Bird Banding News. 50: 83-93.

Stiles, Gary; Skutch, A. 1989. A guide to the birds of Costa Rica. Ithaca, NY: Cornell University Press. 511 p.

Will, Thomas C. 1986. The behavior ecology of species replacement: Blue-winged and Golden-winged warblers in Michigan. Ann Arbor, MI: University of Michigan. 126 p. Ph.D. dissertation.

Jose' Luis Rangel Salazar

Forest habitat at La Selva Biological Station, Costa Rica.

Increasing Mist Net Captures of Migrant Northern Saw-whet Owls (*Aegolius acadicus*) with an Audiolure

Thomas C. Erdman and David F. Brinker[1]

Abstract.—In 1986, an "audiolure" was developed and tested at the Little Suamico Ornithological Station near Green Bay, Wisconsin. The audiolure consisted of broadcast amplified "solicitation" calls of Northern Saw-whet Owls (*Aegolius acadicus*) normally associated with courtship activities. From 1971 through 1985, using passive mist netting at Little Suamico, the mean number of owls captured each autumn was 57. Using an audiolure, from 1987 through 1995, the mean annual catch was 636 owls. During 1989, an audiolure was also tested at Finzel Swamp in western Maryland by comparing captures during adjacent 3-hour time blocks. Use of an audiolure significantly increased capture rates over passive mist netting. Audiolures are now being used by all major Northern Saw-whet Owl banding stations in the western Great Lakes area to net 2,000-3,000 owls each autumn. Audiolures have also proven effective for netting saw-whet owls during both the breeding and wintering seasons. Descriptions of the audiolure and basic characteristics of captures at simple autumn migration netting operations are also presented.

Each year more Northern Saw-whet Owls (*Aegolius acadicus*) are banded in North America than any other owl species. In the Great Lakes region 2,000-3,000 are banded during each autumn migration. It has been assumed that these small owls, like most diurnal raptors, are reluctant to cross large bodies of water and that they concentrate along certain shorelines. Most bird watchers, unfamiliar with the results at banding stations, still consider saw-whet owls rare and a "great find."

Taverner and Swales (1911) suggested that Northern Saw-whet Owls were migratory during the early 1900s. The first published attempt at capturing and studying numbers of migrant Northern Saw-whet Owls came from the Cedar Grove Ornithological Station located along the Wisconsin shoreline of Lake Michigan. Mueller and Berger (1965) reported that "numbers" of these then "rare" owls could be captured with mist nets left open at night. Using that technique they documented a pronounced autumn migration during October and November, confirming Taverner's (1911) suggestions.

Since the 1960s many other banding stations have tried mist netting migrant owls, with varying degrees of success. The use of mist nets to capture migrant owls has been a passive technique. A general rule of passive mist netting is that to capture more individuals, one must operate more nets and cover more area. This paper details our development and use of audiolures to increase mist net captures of migrant Northern Saw-whet Owls. Use of audiolures significantly increases captures of migrant saw-whet owls while simultaneously allowing a reduction in the number of nets that must be maintained and operated.

STUDY AREAS AND METHODS

The breakthrough was developed in 1986 at the Little Suamico Ornithological Station (LSOS) along the western shore of Green Bay, 17 km north of Green Bay, Wisconsin. Additional testing of the audiolure was conducted in 1989 at Finzel Swamp in the mountains of the Allegheny Plateau, 16 km west of Cumberland, Maryland. Data are also included from banding stations at Assateague Island along the Atlantic Coast, 22 km south of Ocean City, Maryland and along the Casselman River, 40 km southwest of Cumberland, Maryland. A detailed description of the Little Suamico Ornithological Station can be found in Brinker and Erdman (1983).

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At all sites the mist nets used to capture Northern Saw-whet Owls were 12 m, 61 mm mesh. At LSOS, where nets are part of a diurnal raptor banding operation, nets remained open continuously. Maryland stations opened nets at dusk and closed them at dawn. At all stations, nets were checked frequently throughout the night. Nets were not opened during inclement weather.

The initial effort to capture migrant owls at LSOS consisted of placing nets in various locations thought to be good "flight lanes" for owls. In the search for good net sites, various single, double, and triple high net configurations were tried at different locations throughout the years from 1971-1986. This effort peaked at 38 nets in 1978. The audiolure was first used in 1986. Since then, at LSOS all use of nets in outlying areas has ceased, the number of nets operated each year has been reduced by 65 percent, and has remained stable at 12-13 nets.

Netting efforts at Finzel began in 1986 with 10 nets at three sites around the swamp. During 1987, 18 nets were placed in a single area, and by 1988 the effort consisted of 25 nets in an essentially continuous line along a single lane gravel road that crossed the swamp. The line of nets was established to investigate differential habitat use. An audiolure was first used at Finzel during 1989. The net line was reduced to six nets with an audiolure in 1990, and use of this site ceased after 1990. Studies began at Assateague in 1991 and at Casselman River in 1992. Audiolures were used at both Assateague and Casselman since establishment and these sites each operate 6-7 nets annually.

Design of our audiolures varied, but has stabilized around lures that produce sound pressure levels of 100-110 dB at 2 m. On calm nights, at this sound pressure level most people can hear the lures at distances of more than 1.5 km. Audiolures replay the primary solicitation calls of Northern Saw-whet Owls recorded on 3-minute continuous loop tapes. Several tapes with differing call sequences have been used with equal success. All tapes have quiet periods on them, some as long as 30 seconds. Construction details and a schematic of the audiolure are included as an appendix.

As a final test of the audiolure's effectiveness, a rigorous sampling design was applied to its operation at Finzel during 1989. The audiolure was operated on alternate nights during one of two randomly selected 3-hour blocks, either dusk-21:00 or 21:00-midnight. There is a strong seasonality component to capture rate effect. Early in the season capture rate is low and by mid-season it is high, capture rate then declines as the season progresses and comes to a close. Seasonality is not a linear effect, it is most similar to a quadratic relationship. The sampling design controlled for seasonality by treating each test night as a replicate. The design also controlled for major variation in weather effects that differed between test nights. Variation from weather effects occurring during the dusk-midnight period and time-of-night effects were relegated to random error. The difference between the two treatments, lure on or lure off, was tested with Analysis of Variance using SAS' General Linear Model (GLM). Although a Paired T-test could have been used to simply test for treatment effect, the GLM approach was used to facilitate providing an estimate of the total number of owls that would have been trapped during the 1989 season with and without the use of an audiolure. GLM was used to output daily predicted values for both treatments. To obtain the total for the season, daily predicted values were summed by treatment. When the GLM was run, date was a significant effect and the quadratic expression of date very closely approached significance.

RESULTS

The simplest and most dramatic test of the effectiveness of the audiolure was the significant difference in total annual captures at LSOS between the 1971-1985 passive netting period and 1987-1995 audiolure period ($F = 415.67$, $P < 0.0001$, fig. 1). The mean number of owls captured in the passive netting period was 57 (range 15-108). The greatest number of owls captured during the passive netting period occurred in 1978, the year when the maximum number of nets was operated. During the audiolure period the mean number of owls captured was 636 (range 526-864).

The test at Finzel Swamp also showed that an audiolure used with mist nets captured significantly more saw-whet owls than passive mist

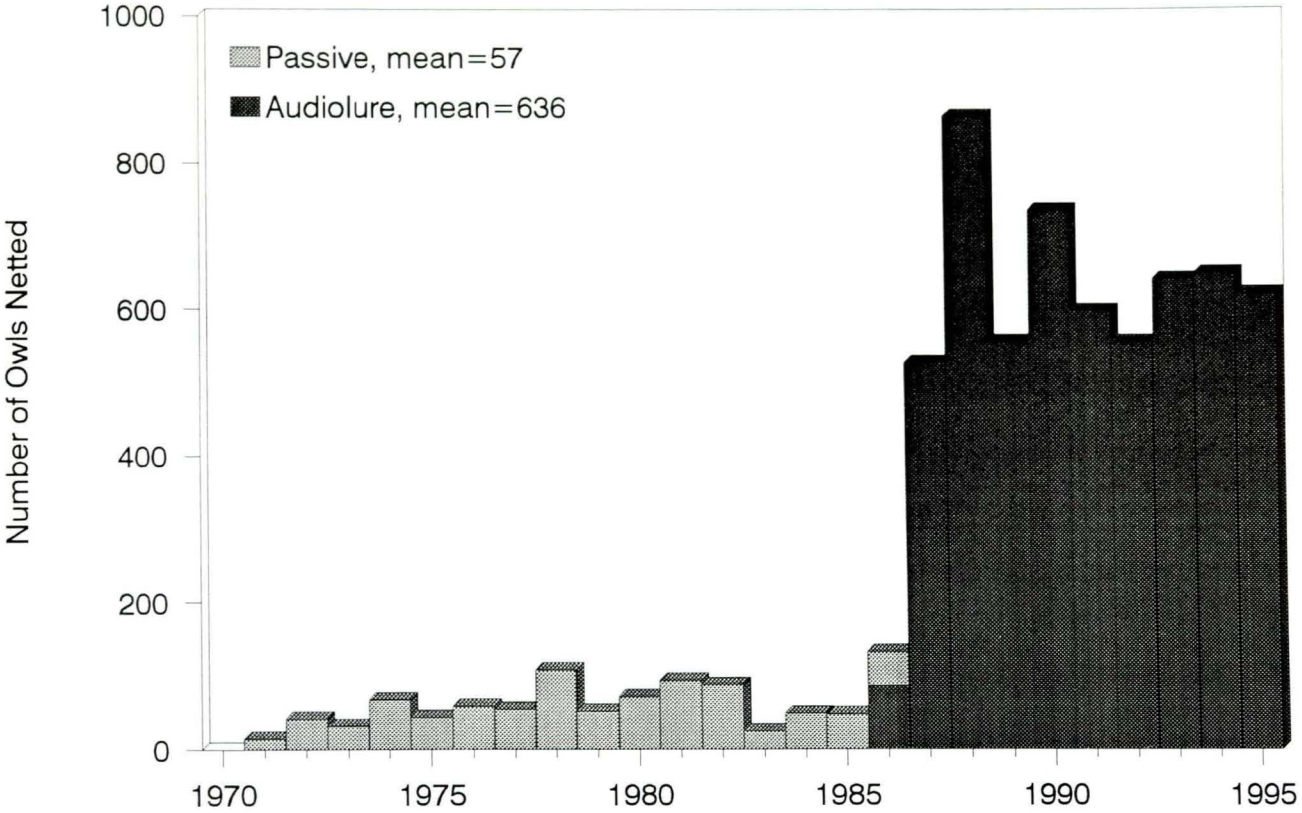


Figure 1.—*Captures of Northern Saw-whet Owls* (Aegolius acadicus) *at the Little Suamico Ornithological Station near Green Bay, Wisconsin from 1971 through 1995. The difference between passive and audiolure mist netting was highly significant (F = 415, df = 23, P < 0.0001).*

netting (F = 6.08, P = 0.002). Figure 2 summarizes the predicted number of owls captured in 5-day periods by treatment. The ANOVA model predicted an increase in captures by a factor of 4. From 1986 through 1988 the highest annual capture of saw-whet owls while using passive netting was 36 (in 1987). During 1989, 65 Northern Saw-whet Owls were captured at Finzel. Including recaptures, 61 percent of the captures occurred during audiolure periods, although the audiolure was used only 16 percent of the time that nets were open. During 1990, an audiolure was used throughout the season, the number of nets operated was reduced from 25 to 6, netting was reduced from dusk-dawn to dusk-midnight, and 114 saw-whet owls were captured.

From establishment of the stations at Assateague Island and Casselman River through the autumn of 1994, these two stations netted a combined total of 465 Northern Saw-whet Owls. In the east, the autumn 1995 migration was exceptional, and 628 saw-whet owls were banded at these two stations. The net arrays at both stations are similar: a relatively straight east-west line of six or seven nets. The distribution of captures by net at these stations is summarized in figure 3, with 1995 depicted separately from preceding years. Little difference was observed in the distribution of captures between 1995 and earlier years. Captures decline as distance from the audiolure increases. The results from Casselman River show a similar relationship near the audiolure but were complicated by a non-homogeneous habitat. The height of capture by net deck at Assateague and Casselman River is summarized in figure 4. Again 1995 data are presented separately from previous years. Most captures (67 percent) occurred within 2 m of the ground, i.e., the bottom net of a two net high rig, and captures decreased substantially above 2 m.

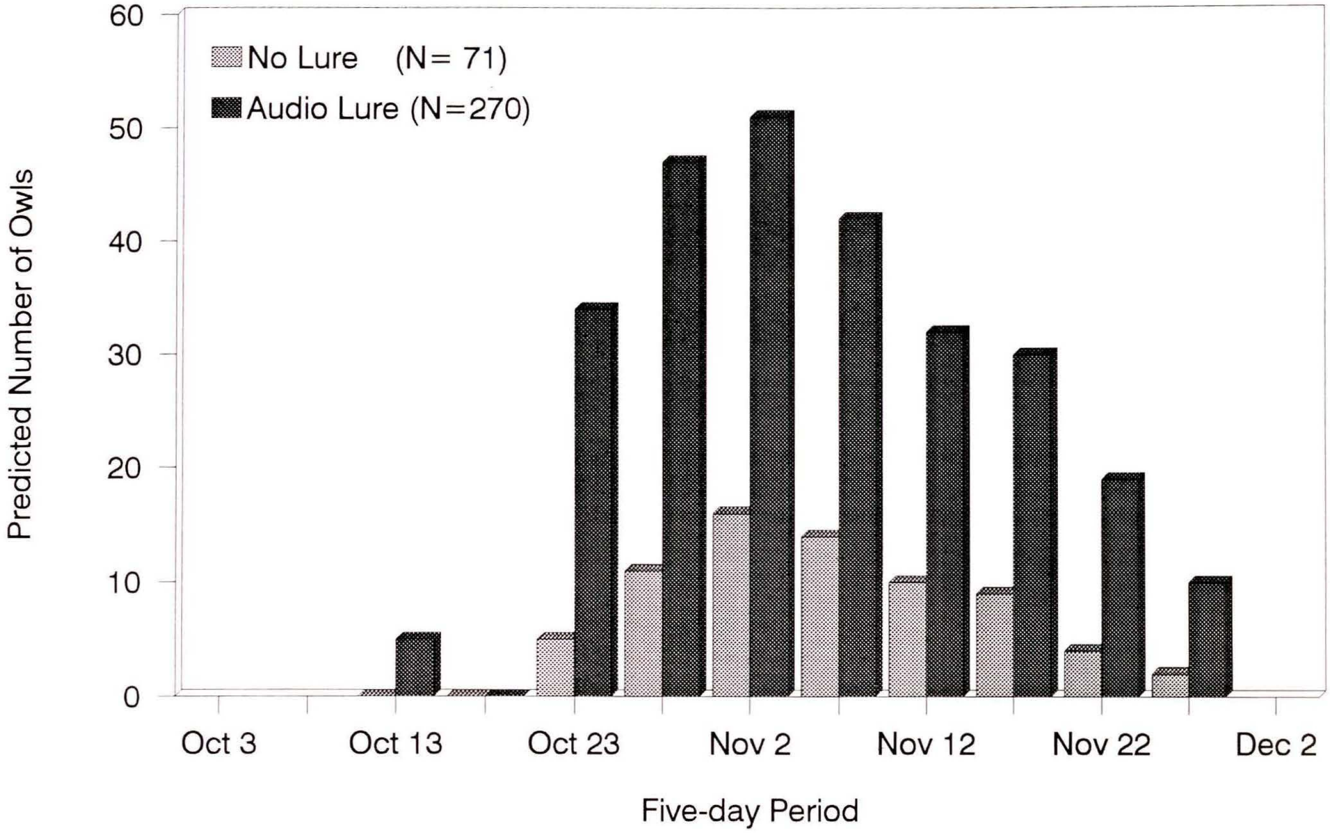


Figure 2.—*Predicted number of Northern Saw-whet Owls* (Aegolius acadicus) *netted by 5-day period at Finzel Swamp, Maryland during 1989. The difference between passive and audiolure mist netting was significant (F = 6.11, df = 30, P = 0.002). N = the total number of owls predicted for each treatment.*

DISCUSSION

Owl Captures

Using an audiolure significantly increased the capture of migrant Northern Saw-whet Owls over passive netting. Captures at LSOS increased by an order of magnitude, while the number of nets was reduced by approximately 65 percent. Increases in capture rates at Finzel Swamp, although smaller in magnitude, were also highly significant. Before work at Finzel Swamp, mist netting directed toward migrant Northern Saw-whet Owls had not been attempted in Maryland. Without the use of an audiolure, banding of migrant saw-whet owls would not be practical in Maryland or further south. Other researchers are now netting significant numbers of Northern Saw-whet Owls at sites where previous attempts had failed (E. Jacobs, pers. comm.). Several of these are not near any hint of a classical leading line, such as a shoreline or mountain ridge.

The audiolure is presumed to increase captures by attracting owls to the vicinity of mist nets from considerable distances and by increasing the time owls spend near the nets. Increased residency time near the nets significantly increases the probability of capture. This results in a considerable increase in captures above that of passive mist netting. Because of the strong attractive influence of the audiolure, capture rates at banding stations using audiolures are probably more indicative of larger scale regional and geographic influences than small scale local habitat effects.

The significant increase in captures with use of the audiolure indicated that a small proportion of the possible migrants was being netted with passive techniques. Undoubtedly this proportion has increased since use of audiolures became routine. However, the increase may not be as great as one might suspect. It is apparent from vocalizations that an unknown proportion of the migrants attracted to the vicinity of the mist nets are not being netted.

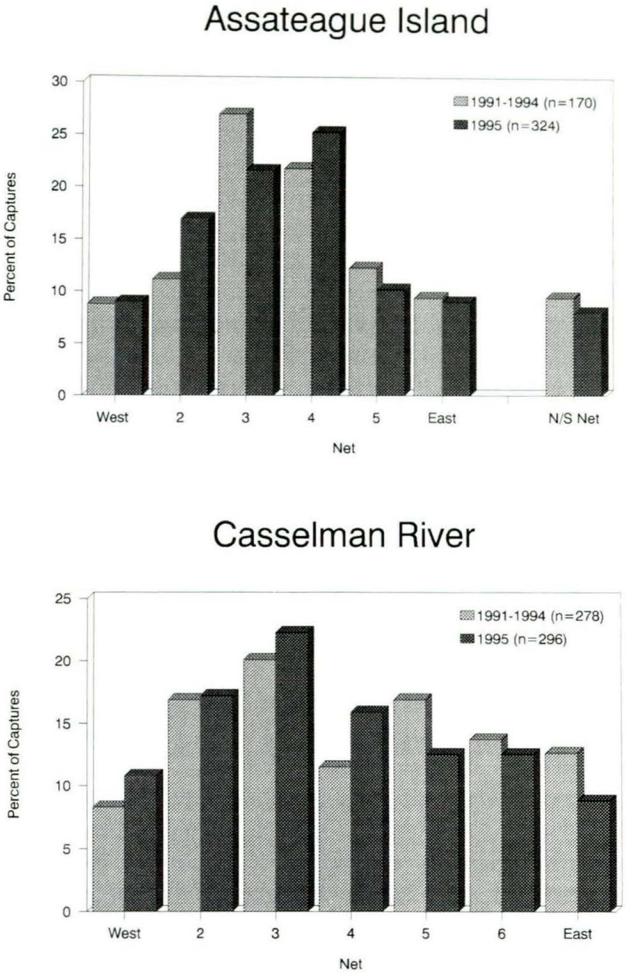


Figure 3.—*Distribution of Northern Saw-whet Owl (*Aegolius acadicus*) captures by mist net using an audiolure at two autumn migration stations, Assateague Island and Casselman River, Maryland, 1991-1994. An exceptional migration occurred during 1995 and these data are reported separately. N = total number of owls for that station and period. N/S refers to a single perpendicular net mid way along the north side of the net line. At Assateague Island the audiolure was positioned at the junction of nets 3, 4, and the N/S net. At Casselman River the audiolure was positioned near the middle of net 4.*

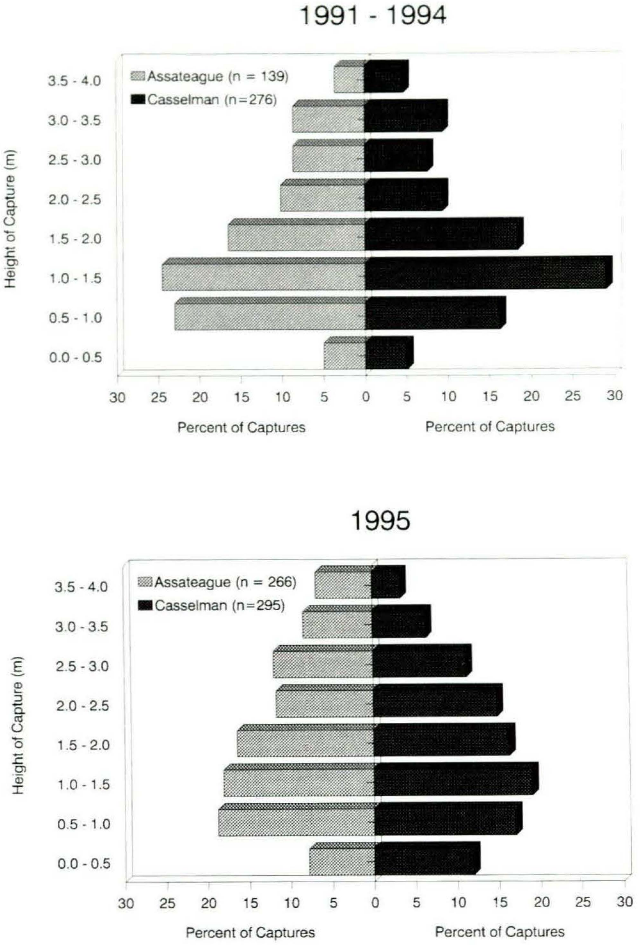


Figure 4.—*Distribution of Northern Saw-whet Owl (*Aegolius acadicus*) captures by height using an audiolure at two autumn stations, Assateague Island and Casselman River, Maryland, 1991-1994. An exceptional migration occurred during 1995 and these data are reported separately. N = total number of owls for that station and period.*

As with any improvement in a technique, new problems arise. One complication was housing large numbers of owls until they could be processed. A system of small boxes or mesh bags to individually hold owls is essential. For example, in Wisconsin it is not unusual to have one or more nights per season when over 50-75 saw-whet owls are netted in a night. In cases like this, additional personnel are absolutely necessary to tend nets properly and process birds. Another problem has been the increased threat from ground predators and larger owls. Mammals, such as common striped skunks (*Mephitis mephitis*), raccoons (*Procyon lotor*), red foxes (*Vulpes fulva*), opposums (*Didelphis virginia*), and feral cats (*Felis domestica*) have become major threats. The same is true for both resident Great Horned Owls (*Bubo virginianus*) and wandering Barred Owls (*Strix varia*). We now have to live trap and remove predators from the netting area continuously.

Observations on the distribution of captures will be useful to others initiating use of an audiolure to net migrant Northern Saw-whet Owls. In Maryland, we use essentially similar net arrays at each banding station. These consist of approximately straight lines of 6 or 7 nets. In homogeneous habitats, such as the open Loblolly Pine *(Pinus taeda)* forest at Assateague Island, captures concentrate at the nets closest to the audiolure speakers (nets 3 and 4 at the center of the net line) and decrease as distance from the speaker increases (fig. 3). A more complicated pattern was found at Casselman River where the habitat is not homogenous along the net line. These nets have been set up in a small clearing in a grove of eastern hemlock (*Tsuga canadensis*). Here, a dense stand of hemlock lies immediately south of nets 1 and 2, and there is a large red spruce (*Picea rubens*) immediately north of the junction of net 2 and 3, and nets 3-7 are in a small clearing with scattered hawthorn (*Creategus sp.*). Although the speaker was near the center of net 4, there was a very strong tendency to capture owls on the western end of the net array near the large red spruce and dense hemlocks. Northern Saw-whet Owls netted during migration at these sites tend to be low, with approximately 65 percent caught in the bottom net of 2-net high sets. The capture height at Casselman River is slightly higher than at Assateague because of the large red spruce north of net 3.

Audiolures have great potential to improve capture techniques for other species. We have found it to work for Eastern Screech- (*Otus asio*), Boreal (*Aegolius funereus*), Great Horned, and Barred Owls. Audiolures placed atop walk-in traps has also significantly improved capture success for migrant Soras (*Porzana carolina*). Annual captures used to be less than 35-40 individuals and now more than 500 are captured each season (G. Kearns, pers. comm.).

Portable audiolures can easily be used for other applications such as playback response survey and census efforts. We have used an audiolure successfully to mist net wintering Northern Saw-whet Owls as part of a mark recapture experiment on Assateague Island. We have also netted individual owls and family groups during the summer breeding season with the use of a mist net and audiolure.

Audiolure Construction

Construction and operation of an audiolure is relatively simple and inexpensive. The total cost of a recorder, storage battery, battery charger, amplifier, voltage converter, and outdoor speakers is approximately $200-$300 (U.S.). Good deep-cycle rechargeable 12v DC wet cells (RV/Marine battery) will last 10 to 14 days without recharging. For an additional $100 or so, a solar panel can be used to recharge the 12v battery in remote locations where 120v AC current is not readily available. An alternative power source is a sealed rechargeable lead-acid battery, commonly used for home security systems. These small batteries (9 x 11 x 7 cm) provide 4 amp-hours of current and are sufficient to run the audiolure for a 12 hour period. They can be recharged in approximately 4 hours. With a few extra accessories, it is also possible to run the audiolure from the cigarette lighter of a nearby vehicle. We recommend not wasting money trying to use standard C or D sized dry cells made for use in portable tape recorders. Even the most expensive dry cells seldom last more than one night, while a good quality 12v battery charger can recharge a wet cell in 12-24 hours. The tape used is a 3-minute continuous loop used in telephone answering machines, and costs about $5.00. Shorter loops are available, but they wear out much faster because of the increased number of times that the loop is played per night compared to the 3-minute loop. Just about any speaker will suffice, provided it is of sufficient wattage that it will not be ruined by over-powering and that it is properly protected from the elements.

For permanent sites, we build a weatherproof wooden shelter to house the audiolure. This shelter contains the battery, amplifier, tape player, and other electrical components. Standard coaxial speaker cable is run from the shelter to the speakers. For portable rigs, we use the small sealed lead acid batteries. Along with the other components, everything for a portable rig can be easily carried in a small backpack.

The actual saw-whet owl vocalization was recorded from a commercial bird vocalization record. Interestingly, quality of the call does not seem to matter to the owls, as considerable success was achieved by an associate using a tape recorded whistled imitation.

A schematic of the wiring necessary for an audiolure is presented in the appendix. The schematic illustrates the basic connections necessary to run the tape player and amplifier off a single power source. Either a mono or a stereo tape player can be used. The schematic illustrates wiring for when a mono tape player is used. In that case, the input to the right and left channels must be combined. When a stereo tape player is used, these wires are not connected together. We wire the system so that components are easily replaceable by using jacks and other electrical connectors rather than soldering all connections directly. This allows for quick and easy replacement of any components that may malfunction in the field. When several audiolures are available, this makes it easy to correct problems by simply swapping parts from an unused system.

ACKNOWLEDGMENTS

Over the years many people have assisted in our efforts to study Northern Saw-whet Owl migration; to all of those not mentioned here we offer our most sincere thanks for their contributions of time and effort. Throughout the years, a major contribution to LSOS has been made by our spouses, who have shown unusual support for our addiction to the study of raptor migration. R. Rost, the dairy farmer whose woods and pastures we have occupied since 1971, has been a continual friend tolerant of our unusual activities. Over the last 26 years others who deserve recognition are the assistants, i.e., "gabboons" and moral supporters, without whose help it would have been impossible to maintain thorough annual coverage. In Wisconsin, these people included, D. Erdman, J. Jacobs, G. Zuberbier, J. Steffen, J. Trick, G. Henklemann, B. Haug, and T. Meyer. In Maryland, major contributions were made by J. McKearnan, K. Dodge, J. McConnaughey, G. Shire, and many students from Frostburg State University and Garrett Community College. Funds for work in Maryland were obtained from grants to D. Brinker, J. McKearnan, and K. Dodge by the Maryland Ornithological Society and through in-kind contributions of equipment and housing by the Maryland Department of Natural Resources and Assateague Island National Seashore. Permission to operate on lands under their control was graciously provided by the Maryland Chapter of The Nature Conservancy (Finzel Swamp) and Assateague Island National Seashore.

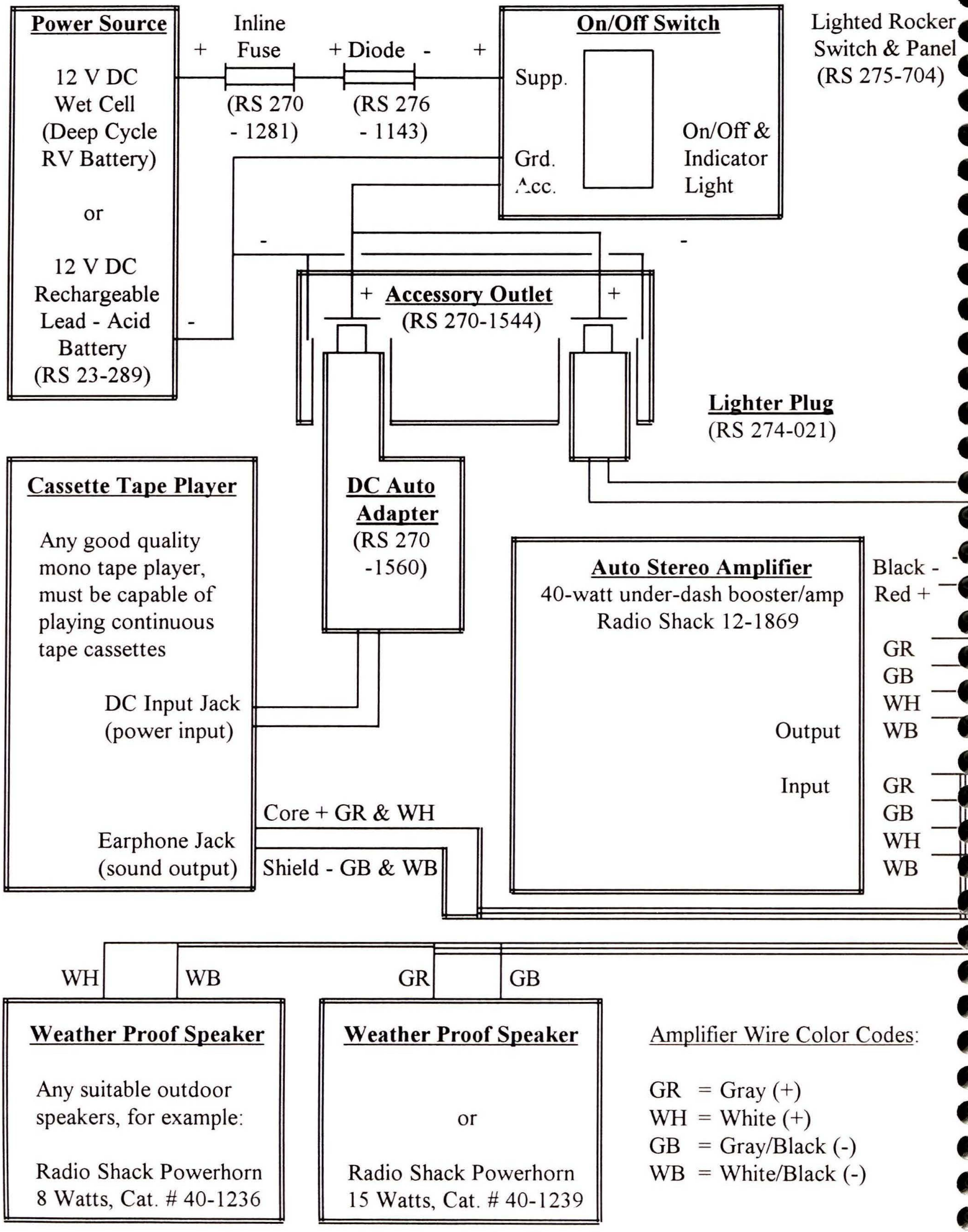
LITERATURE CITED

Brinker, D.F.; Erdman, T.C. 1983. Characteristics of autumn Red-tailed Hawk migration through Wisconsin. In: Proceedings of hawk migration conference 4; 1983 March 24-27; Rochester, NY: 107-136.

Mueller, H.C.; Berger, D.D. 1965. Observations on migrating Saw-whet Owls. Bird Banding. 28(2): 120-125.

Taverner, P.A.; Swales, B.H. 1911. Notes on the migration of the Saw-whet Owl. Auk. 28(3): 329-334.

Appendix A.—Audiolure schematic, parts list, and construction notes.


Power Source
12 V DC
Wet Cell
(Deep Cycle
RV Battery)
or
12 V DC
Rechargeable
Lead - Acid
Battery
(RS 23-289)
+
Inline
Fuse
(RS 270
- 1281)
+ Diode -
(RS 276
- 1143)
+
On/Off Switch
Supp.
Grd.
Acc.
On/Off &
Indicator
Light
Lighted Rocker
Switch & Panel
(RS 275-704)
-
-
-
+ Accessory Outlet +
(RS 270-1544)
Lighter Plug
(RS 274-021)
Cassette Tape Player
Any good quality
mono tape player,
must be capable of
playing continuous
tape cassettes
DC Input Jack
(power input)
Earphone Jack
(sound output)
DC Auto
Adapter
(RS 270
-1560)
Core + GR & WH
Shield - GB & WB
Auto Stereo Amplifier
40-watt under-dash booster/amp
Radio Shack 12-1869
Black -
Red +
Output
GR
GB
WH
WB
Input
GR
GB
WH
WB
WH
WB
GR
GB
Weather Proof Speaker
Any suitable outdoor
speakers, for example:
Radio Shack Powerhorn
8 Watts, Cat. # 40-1236
Weather Proof Speaker
or
Radio Shack Powerhorn
15 Watts, Cat. # 40-1239
Amplifier Wire Color Codes:
GR = Gray (+)
WH = White (+)
GB = Gray/Black (-)
WB = White/Black (-)

(Appendix A continued)

PARTS LIST

Major Components	Cat. No.	Price	Notes:
Any good quality tape player (for ex. Radio Shack)	14-1156	$49.99	mono
40 Watt Auto Stereo Amplifier	12-1869	$19.99	
Powerhorn Outdoor Speakers			
8 Watts **or**	40-1236	$43.98	cost is for 2
15 Watts	40-1239	$67.98	cost is for 2
Universal DC Auto Adapter	270-1560	$12.99	
Other Components			
Flip Switch/Light Panel	275-704	4.49	On/Off switch
Triple Accessory Outlet	270-1544	9.99	for power supply
Lighter Plug	274-021	3.49	or RS 274-331
In line Fuse Holder & Fuse	270-1281	1.59	
Diode	276-1143	1.19	
1/8" Mono Plug - 2 RCA Phono Jacks	42-2154	2.49	Y Adapter
RCA Phono Plugs (pkg. of 4)	274-319A	1.99	4 males required
RCA Phono Jacks (pkg. of 4)	274-337	2.59	2 females required
Quick Disconnect Connectors	64-3049	1.49	misc. connections
Heat Shrink Tubing Assortment	278-1627	1.99	misc. short protection
18 Gauge R/B Wire	278-567	4.19	misc. wiring needs
Endless Loop Cassette Tape (3 min. preferable)	EC-3M	3.78	suggest TDK
Tape Player Cleaner	44-1116	3.99	
12v Deep Cycle Wet Cell Battery (for ex. Sears RV-Marine)	96493	$75.00	

* * * * * * * * * * * * * * * * *

Nominal Cost - all components purchased new, battery and tape player already available, substitute speakers also available	$76.24
Minimum Cost - all components purchased new, battery and tape player available, two 8 watt speakers	$120.22
Average Cost - all components purchased new, battery and tape player available two 15 watt speakers	$144.22
Maximum Cost - all components purchased new, Radio Shack Tape Player	$269.21

(Appendix A continued)

CONSTRUCTION NOTES

Almost all parts can be purchased from Radio Shack. In the schematic and parts list, RS 000-000 or (RS 000-000) represent Radio Shack part numbers. Other supply houses sell comparable parts for similar costs.

The following instructions and notes assume use of a mono tape player and construction of an audiolure that is designed to be housed in an outdoor shelter, such as a weatherproof wooden box. Common deviations will also be included. The instructions will include use of materials that allow quick disassembly and replacement without soldering, as much as possible, to facilitate quick field repairs.

Because this is a direct current (DC) system, throughout construction correct polarization is essential. If polarity is incorrect, components will not operate or may be damaged. This is particularly true of the tape player and amplifier. If audio input/output from the tape player and amplifier it is not correctly polarized, a noticeable loss of volume will occur and the amplifier may be damaged. The safest way is to test the tape output with a volt meter to determine polarity. A usually adequate compromise is to use preconstructed components and shielded cable.

Begin with the amplifier. There are ten wires that exit the back of the amplifier. The red and the black wires are for the power input. Red is positive (+) and black negative (-). Take the red wire (+) from the amplifier and slide a piece of the appropriate diameter heat shrink tubing over the wire. Connect the red wire to the (+) wire of the lighter plug and soldier together. Once the joint is cool, slide the heat shrink tubing down over the connection and shrink the tubing by holding it over a candle flame. Place heat shrink tubing over the black wire, connect the wire to the (-) wire of the lighter plug, soldier together, etc. If you want to make this connection stronger and more resistant to breakage from rough handling, do the following. Before connecting the wires together, place a larger diameter piece of heat shrink tubing over the wire from the lighter plug. After making the connections of the red and black wires, including shrinking the small diameter pieces of tubing over them, slide the large diameter tubing over the two smaller pieces and shrink it down also. This will provide a relatively strong connection that can withstand much abuse.

For use with either a mono or stereo tape player, connect RCA phono plugs (♂) to the input wires of the amplifier. Take a red plug for the right channel input wires (gray & gray with black strip) and unscrew the plastic cover. Notice that negative (-) wires have the black stripe. Feed the two wires through the cover. Connect the gray (+) input wire to the short tab and soldier it. Connect the gray-black (-) input wire to the long tab and soldier it. Lay the two wires against the long tab and squeeze the tab's wings around the pair of wires to lessen the risk that the wires will be pulled from their connections. Slide the cover down and screw it on tight. Take a black plug for the left channel input wires (white & white with black stripe) and connect the plug as described for the right channel. To "fool proof" the amplifier, use RCA jacks (♀) for the output wire connections. Take a red jack (♀) for the right channel output wires (gray & gray with black stripe) and unscrew the plastic cover. Feed the two wires through the cover. Connect the gray (+) output wire to the short tab and soldier it. Connect the gray-black (-) output wire to the long tab and soldier it. Complete as with input plugs.

(Appendix A continued)

When connecting the amplifier to a mono tape player, plug the Y adapter into the earphone jack of the tape player. Then plug the two RCA phono plugs from the amplifier input into the two jacks of the Y adapter. This will direct audio output to both channels of the amplifier. For a stereo tape player purchase a 1/8" stereo plug - 2 RCA phono jack adapter (RS 274-369, $3.59). Substitute this for the Y adapter.

The speakers come with bare wire ends. Connect a RCA phono plug (♂) to each of the speakers. The wire with the white stripe is the positive (+) wire that goes to the short tab. The wire without the stripe is the negative wire that goes to the long tab. To locate the speakers at a distance from the audiolure, use shielded speaker cables with plugs (♂) and jacks (♀) at opposite ends, for example RS42-2363, a 12 foot cable ($3.49).

There are a variety of options for connecting the amplifier and tape player to a power source. For example, one of the simplest is to operated the audiolure from the cigarette lighter of a vehicle. Purchase a DC-Y adapter (RS 270-1535, $5.99) and plug it into the vehicle's cigarette lighter outlet. Then plug the amplifier into one of the two outlets. Plug the universal DC auto voltage adapter into the other outlet. Set the voltage on the DC adapter to the correct setting for the tap player being used (often 6v). Set the polarity of the adapter output to match that required for the tape player. Connect the tape player to the amplifier, connect up the speakers, and the audiolure is set to operate. For use with a 12v wet cell in a weatherproof box, additional wiring is necessary.

Mount the on/off switch and the triple accessory outlet at some convenient location on the inside of the box. Use the 18 gauge supply wire to make the following connections. To obtain red and back wires, the 2-connector supply wire can be split. Throughout the following, all bare connections should be protected with either heat shrink tubing or electrical tape to prevent shorts. Crimp a female quick connector to a red piece of the supply wire. Soldier the opposite end to the negative (-) side of the diode. The purpose of the diode is to prevent equipment damage if the battery is connected with the polarity reversed. To the positive end (+) of the diode attach one end of the fuse holder (polarity is not important). The opposite end of the fuse holder is attached to the positive pole of the battery, either directly or via a second piece of supply wire. The completed audiolure draws a current of less than 0.5 A and a 2 or 3 amp quick blow fuse is sufficient protection. The female quick connector is connected to the supply (supp) tab of the on/off switch. Crimp female quick connector to a piece of black supply wire. To the opposite end, soldier two more pieces of black supply wire. One end of the two black wires is connected to the negative (-) pole of the battery. The other black wire is soldiered to the black (-) wire on the triple accessory outlet. The female quick connector is connected to the ground (grd) tab of the on/off switch. Lastly take a piece of red supply wire and crimp a female quick connector to one end. Soldier the other end to the red (+) wire of the triple accessory outlet. Connect the female quick connector to the accessory (acc) tab of the on/off switch. Plug the DC adapter and amplifier power supply plugs into the triple accessory outlet and proceed as described for powering from a vehicle.

(Appendix A continued)

ADDITIONAL SHORT NOTES:

Only one in-line fuse needs to be purchased, a second comes with the amplifier. Two fuses are used for added equipment protection. With added risk to equipment, a small cost savings can be obtained by only using the fuse supplied with the amplifier. This puts the tape player at some risk. Some lighter plugs and DC voltage adapters come with fuses in their tips. If power problems are encountered, check fuses , including those in plug tips.

A cost savings can be obtained by eliminating the on/off switch. To turn system on/off the battery must then be connected/disconnected each time, or plugs pulled from the accessory outlet.

The diode is highly recommended. It protects equipment from damage due to cross polarization when the battery leads are connected to the wrong battery poles. Basically it is very cheap insurance (i.e. additional "fool proofing")! However, if installed backwards the audiolure will not work.

Any suitable means of connecting the various components can be substituted for the triple accessory outlet and lighter plug used here. The recommended arrangement preserves the most flexibility in other uses of the equipment, such as from an auto cigarette lighter.

Be sure to set the DC power adapter for the correct voltage. Also be certain that the polarity of the input jack is correct to avoid damaging the tape player. The tape player will not operate properly if the voltage is too low or the polarity incorrect!

To cut costs, any available 8 ohm speakers can be used. Generally, the higher the wattage of the speakers, the more volume and thus the better the system will perform (i.e. attract owls). Combined wattage of the two speakers should not exceed 40 watts. When using lower power speakers, care must be taken not to overpower, and thus ruin the speakers. However, we have found the smaller and less expensive 8 watt speakers to perform as well as or better than the larger 15 watt speakers.

Solder all wire connections for best performance! Twisted poor connections end up being a headache and reduce system performance.

Loop cassettes have more internal friction than regular cassettes and do not work well in some tape players with an auto-stop feature. If you purchase a tape player, first check to see that it plays loop cassettes well. A safer bet is to not purchase one with an auto-stop feature.

A Method for Locating Barred Owl (*Strix varia*) Nests in the Southern Boreal Forest of Saskatchewan

Shanna D. Frith, Kurt M. Mazur, and Paul C. James[1]

Abstract.—Barred Owl (*Strix varia*) nests are often very difficult to locate. We developed a method for locating Barred Owl nests within the boreal forest of central Saskatchewan, Canada. During the nesting period, we located pairs of Barred Owls through call-playback surveys. We returned to the survey location at sunset and listened for vocalizations from the pair. These vocalizations often occurred near the nest, providing an estimate of its location. The following day, prospective-looking nest trees in the area were hit with a stick in order to flush the incubating owl. We searched for seven nests this way, locating five or 71.5 percent of them.

In the boreal forest, Barred Owl (*Strix varia*) nests are very difficult to find. This may be due to a number of factors: they occur in low densities with large home range sizes (Elody and Sloan 1985, Hamer 1988, Mazur 1997); their nest sites are clean and free of signs of their presence (Devereux and Mosher 1982); the incubating owls are rarely visible from the ground; and the nest tree species and nest structures are quite variable including cavities, broken-top snags, and stick nests (Bent 1938, Johnsgard 1988, Mazur *et al.* 1997). As a result, little is known regarding the nesting ecology of Barred Owls in the boreal forest.

One method used to locate Barred Owl nests is to radio-mark adult females and follow them to their nest site (Mazur *et al.* 1997). However, this is a costly and time consuming method, especially if the only focus of radio-marking is to locate nests. Furthermore, radio-marking owls is a relatively invasive means of locating nests.

A variety of methods have been used for locating nesting raptors. A systematic search and mapping of potential nest sites in the pre-nesting period has been used to locate some raptor nests (Hager 1957). Observations of hunting adults or tracking radio-marked prey that were captured and taken back to the nest were methods used by Dunstan and Sample (1972) to locate Barred Owl nest sites.

A number of researchers have utilized vocalizations to cue in on owl nests including Lane and Anderson (1995) for Boreal Owls (*Aegolius funereus*), and Rohner and Doyle (1992) for Great Horned Owls (*Bubo virginianus*). Devereux and Mosher (1984) systematically searched their Maryland study area for Barred Owl nests, while narrowing their search by broadcasting Barred Owl calls to elicit responses in order to localize nesting pairs. However, home range sizes of Barred Owls in the boreal forest of Saskatchewan, Canada, are the largest reported for this species to date (Mazur 1997), and we found that relying solely on call-playback recordings to elicit responses did not narrow the nest search area sufficiently to be effective. During a 4-year study of Barred Owl ecology, we developed a more effective method of locating Barred Owl nests.

STUDY AREA

This method was developed and tested between 1994 and 1996 in the Prince Albert Model Forest located in the southern boreal forest of central Saskatchewan, Canada (53°35' - 54°15'N, 105°05' - 106°45'W). Tree species present in the study area were trembling aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), white birch (*Betula papyrifera*), white spruce (*Picea glauca*), black spruce (*Picea mariana*), tamarack (*Larix laricina*), jack pine (*Pinus banksiana*), and balsam fir (*Abies balsamea*). For a more detailed description of the study area see Mazur *et al.* (1997).

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[1] Box 22, Grp. 5, RR 2, Ste. Anne, MB, R5H 1R2, Canada; Grassland and Forest Bird Project, Box 24, 200 Saulteaux Cres., Winnipeg, MB, Canada; and Saskatchewan Environment and Resource Management, Regina, SK, Canada, respectively.

DESCRIPTION OF NEST FINDING METHOD

This method involved repeated call-playback surveys intended to indicate the general area of a nesting pair of Barred Owls, followed by a modification of the "triangulation and search" technique reported by Rohner and Doyle (1992).

Objective 1.—Location of Territory

Through call-playback surveys, with evenly spaced survey stops 1 km apart along roads, we determined the rough location of Barred Owl territories. Often, the first indication of a territory was the response of a male to the call-playback recording. We either continued the call-playback recording, attempting to elicit a response from the female, or we moved to the next survey location. When both the male and female responded, we noted the direction and the approximate distance from where they called. If no female vocally defended the territory during call-playback surveys the search was abandoned.

The following night, we surveyed the area from which the owl pair appeared to have come from in order to gain a more accurate estimate of the location of the nesting area. If the survey location was close to the nest (~500 m), both the female and the male typically responded within approximately 5 minutes of initiating the call-playback recording. Both male and female often flew to the tape recorded call, with a raucous vocal display including caterwauling. If the response occurred after a longer period of time, the location was likely not within 500 m of the nest. Females did not vocally defend the nest site unless the call-playback recording was broadcast within 1 km of the nest (K. Mazur, unpubl. data).

Objective 2.—Dusk Pair Vocalization

At sunset, we returned to the survey location from which the call-playback recording elicited a rapid response from both owls of the pair. At dusk we found that Barred Owl pairs often participate in a vocal exchange and caterwaul at or near the nest. This may have been a food exchange as observed by Devereux and Mosher (1982), or a form of pair bonding. The direction (azimuth) and approximate distance to the vocalizing owls were recorded.

Objective 3.—Nest Search

The following day, we searched the area where dusk pair vocalizations were heard. The area immediately surrounding suitable looking nest trees was searched for pellets or feathers clinging to branches. Potential nest trees were struck with a large stick. This typically flushed an incubating owl. The presence of a male Barred Owl sometimes indicated that a nest was located in the immediate area. Our search times ranged from 20 minutes to 4 hours. If we were unsuccessful, we would repeat Objective 2 from subsequent listening stations in order to facilitate triangulation of the owls' location.

RESULTS AND DISCUSSION

This method relies on the presence of the adult female on the nest and is therefore only effective during incubation and brooding periods. This is approximately 7 to 8 weeks (Johnsgard 1988) and, in this study area, from early April to mid-June. We avoided keeping females off the nests for long periods to prevent the eggs or chicks from chilling. We recommend avoiding excessive call-playbacks to minimize disturbance to nesting owls.

Of the seven Barred Owl territories identified using this method we located five of the nests, representing a 71.5 percent success rate. In both cases in which we were unable to find the nest, we were also unable to hear a dusk vocal exchange. These two nests may have been too far from the listening location.

We found the dusk vocal exchanges at or near the nest to be important in narrowing the search area. Therefore, a limitation of this method is that the nest must be within the audible range of a survey location. Call-playback surveys and listening for dusk vocal exchanges may need to be undertaken within the forest, in areas of low accessibility, in order to locate nests far from roads. The five nests located using this technique were all within 500 m of the road (mean 250 m). We found this method of locating Barred Owl nests to be effective and recommend its use in the boreal forest.

ACKNOWLEDGMENTS

Funding and support for this project was provided by the Prince Albert Model Forest, Saskatchewan Heritage Foundation, Wildlife Development Fund, Prince Albert National Park, Nature Saskatchewan, and the Northern Forest Owl Symposium Research Award. Robert Warnock kindly provided comments on this manuscript.

LITERATURE CITED

Bent, A.C. 1938. Life histories of North American birds of prey, Part II. New York, NY: Dover Publishing Inc. 482 p.

Devereux, J.G.; Mosher, J.A. 1982. Nesting habits of the Barred Owl in western Maryland. Maryland Birdlife. 38: 124-126.

Devereux, J.G.; Mosher, J.A. 1984. Breeding ecology of Barred Owls in the central Appalachians. Journal of Raptor Research. 18: 49-58.

Dunstan, T.C.; Sample, S.D. 1972. Biology of Barred Owls in Minnesota. The Loon. 44: 111-115.

Elody, B.I.; Sloan, N.F. 1985. Movements and habitat use of Barred Owls in the Huron Mountains of Marquette County, Michigan, as determined by radiotelemetry. Jack-Pine Warbler. 63: 3-8.

Hager, D.C., Jr. 1957. Nesting populations of Red-tailed Hawks and horned owls in central New York State. Wilson Bulletin. 69: 263-272.

Hamer, T.E. 1988. Home range size of the northern Barred Owl and Northern Spotted Owl in western Washington. Western Washington University. 86 p. M.S. thesis.

Johnsgard, P.A. 1988. North American owls. Washington, DC: Smithsonian Institution Press. 295 p.

Lane, W.H.; Anderson, D.E. 1995. Habitat requirements for Boreal Owls in northeastern Minnesota. Final report prepared by Minnesota Cooperative Fish and Wildlife Research Unit, University of Minnesota, for North Central Forest Experiment Station, St. Paul, Minnesota. 52 p.

Mazur, K.M. 1997. Spatial habitat selection by Barred Owls in the boreal forest of Saskatchewan, Canada. Regina, SK: University of Regina. 80 p. M.S. thesis.

Mazur, K.M.; James, P.C.; Frith, S.D. 1997. Barred Owl (*Strix varia*) nest site characteristics in the boreal forest of Saskatchewan, Canada. In: Biology and conservation of owls of the northern hemisphere: 2d International symposium; 1997 February 5-9; Winnipeg, Manitoba. Gen. Tech. Rep. NC-190. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station: 267-271.

Rohner, C.; Doyle, F.I. 1992. Methods of locating Great Horned Owl nests in the boreal forest. Journal of Raptor Research. 26: 33-35.

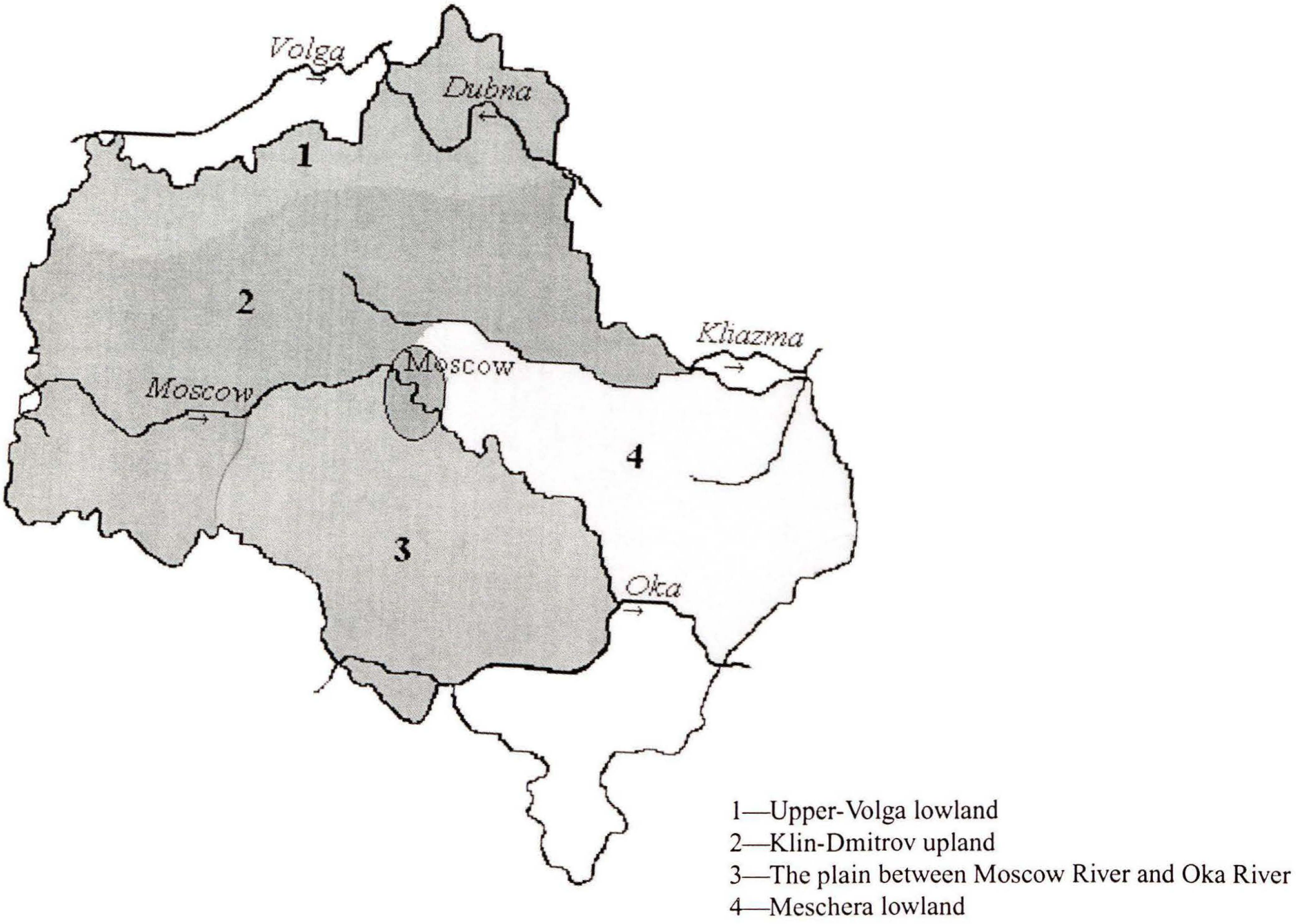
Owls in the Moscow Region: the Results of a 10-year Study

O.S. Grenchenko, S.V.Volkov, and T.V. Sviridova

Abstract.—Owls are one of the least studied groups of birds not only in the Moscow region but throughout Russia. The only detailed essay on owls in the Moscow region is by E.S. Ptushenko and A.A. Inozemtsev (1968),but otherwise no special studies of owls have been carried out here.

Since 1986, the Druzhina for Nature Conservation at the Biology Faculty of Moscow State University has researched owls as a part of the study program on rare birds in the Moscow region. This is the oldest non-governmental student organization for active conservation of old-growth forests, rare animals and plants, and environmental education in the Moscow region.

Many amateur and professional ornithologists took part in this work.


Volga
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1
2
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Moscow
Kliazma
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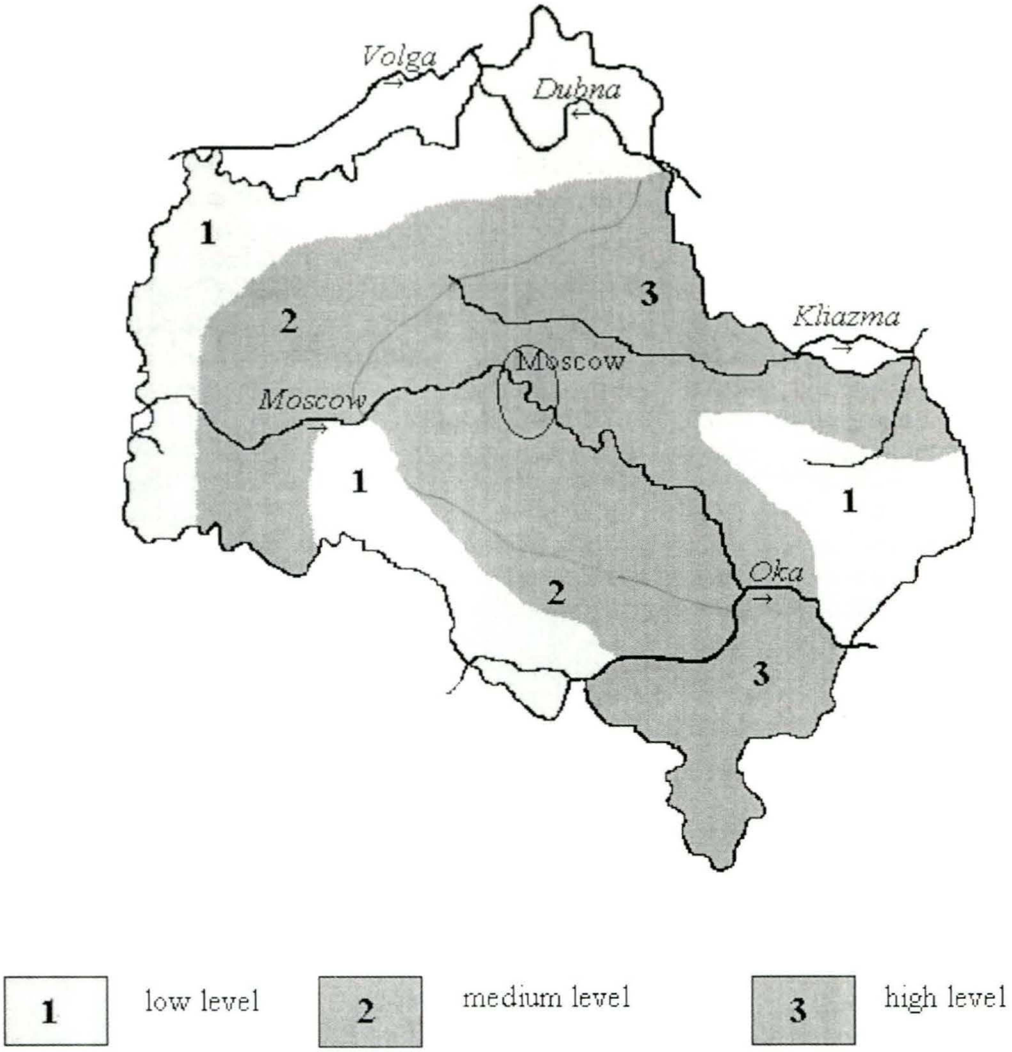
3
Oka
1—Upper-Volga lowland
2—Klin-Dmitrov upland
3—The plain between Moscow River and Oka River
4—Meschera lowland

Figure 1.—*Natural zones of the Moscow region.*


Volga
Dubna
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Moscow
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Oka
1
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1
1
2
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1 low level
2 medium level
3 high level

Figure 2.—*Degree to which natural communitieshave been transformed due to human activity in the Moscow region.*

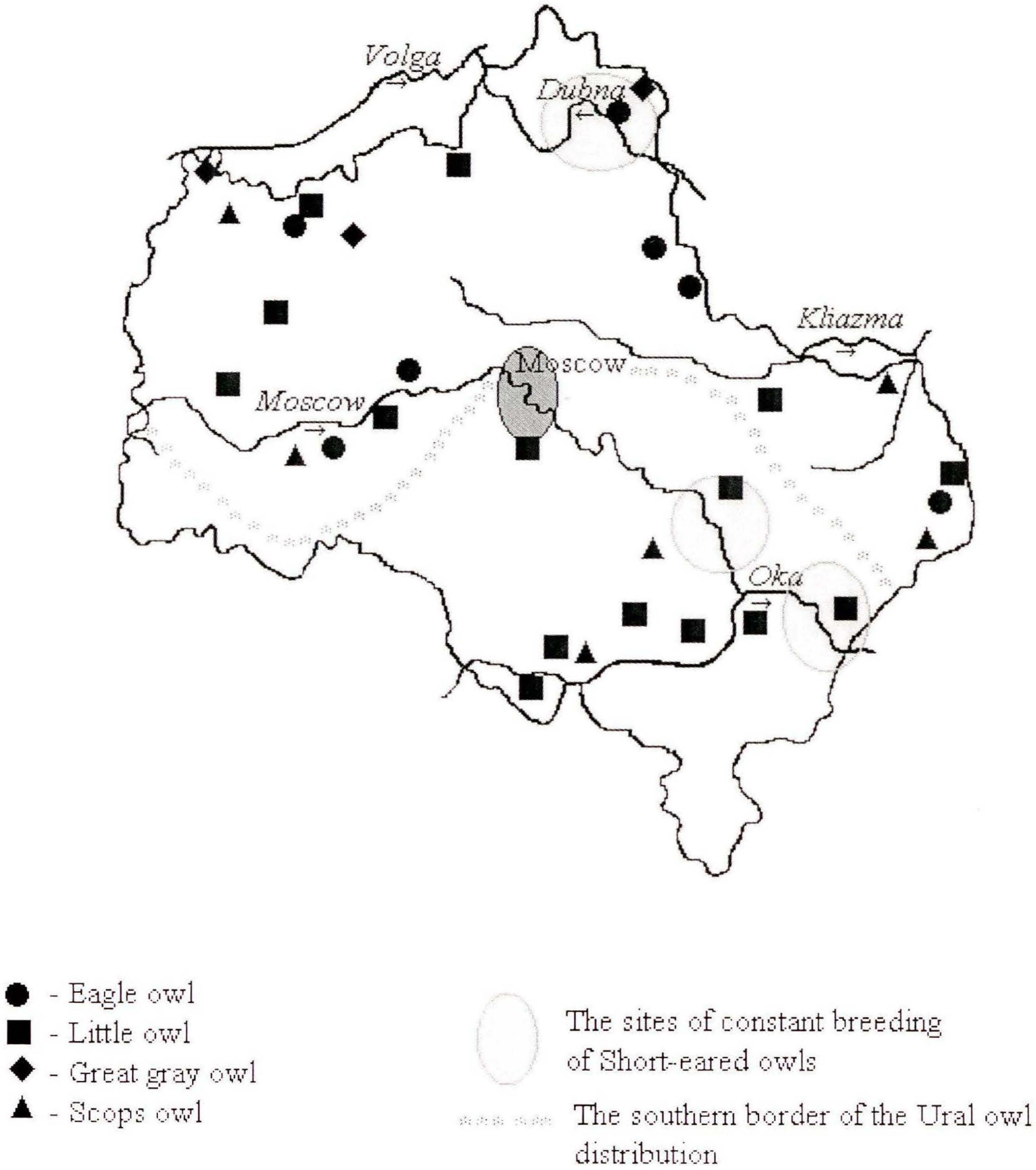
Volga
Dubna
Kliazma
Moscow
Moscow
Oka
● - Eagle owl
■ - Little owl
◆ - Great gray owl
▲ - Scoops owl
The sites of constant breeding of Short-eared owls
The southern border of the Ural owl distribution

Figure 3.—*Distribution of rare owl species in the Moscow region.*

Estimation of Food Consumption from Pellets Cast by Captive Ural Owls (*Strix uralensis*)

Aki Higuchi and Manabu T. Abe[1]

Abstract.—There is considerable data in the literature on the diet of the Ural Owl (*Strix uralensis*) based on pellet analysis. Though it is possible to identify prey items by this method, the volume of food consumption is still unknown. The population of Ural Owls in Japan is declining due to the reduction of old-growth forest and the concurrent loss of natural nest cavities in older trees. More information, including dietary requirements, is needed to conserve suitable habitat and manage for this species. In this study, ingested food and cast pellet mass were quantified to determine if food consumption could be predicted from pellet mass for captive Ural Owls. Three caged adult owls were acclimatized for 2 months. Three common and natural Ural Owl prey species were fed to the captive owls: *Microtus montebelli*, *Apodemus speciosus*, and *A. argenteus*. There was no significant difference in the caloric value for each prey species used. Therefore, the body weight (mass) of prey species was considered a suitable index of food energy. The energy intake by owls was positively correlated with dry pellet weight: estimated calorie intake (kcal) = 33.82 x dry pellet mass (g) + 7.38. The influence of owl activity and seasonal changes in energy budgets on this relationship need to be determined.

The population of Ural Owls (*Strix uralensis*) in Japan is declining due to reduction of old-growth forest. Ural Owls nest in natural tree cavities found in this forest type. It is difficult to directly observe Ural Owls because they are completely nocturnal and their habitat is typically dense forest. But their diet in Japan has been recorded through stomach and pellet analysis (Ikeda and Imaizumi 1949, Imaizumi 1968, Matsuoka 1977). Experiments have shown that Ural Owls cast about one pellet per day (M.T. Abe, unpubl. data). Though it is thus possible to identify individual prey items, the volume of food consumed is still unknown (M.T. Abe, unpubl. data). To better manage Ural Owl populations, it is necessary to understand their habitat and food requirements. As a first step, we performed laboratory studies to determine if the volume of food consumption could be predicted from dry pellet mass.

METHODS

Three healthy, but permanently crippled adult Ural Owls, obtained from a rehabilitation center at Niigata, Japan, were used in this experiment after acclimation for 2 months. The owls were kept in small cages (1.5 x 1.5 x 1 m), and fed weighed amounts of three common and natural prey species at a fixed time (17:00 p.m.) daily. The prey species used in this study were *Microtus montebelli*, *Apodemus speciosus*, and *A. argenteus*. These are considered to be principal food items for Ural Owls in Japan (Ikeda and Imaizumi 1949, Imaizumi 1968, Matsuoka 1977).

Prey species used to feed the captive owls were snap-trapped in the field, weighed and then frozen at -20°F. The rodents were thawed at room temperature, then fed to the owls. Pellets from the owls were picked up, dried and weighed. Thus we determined the relationship between food consumption and dry pellet weight. This study was conducted from 21 November 1994 to 14 February 1995.

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The quality of each prey species used was evaluated as a caloric value per individual. We sampled five each of the three species. After measuring their fresh body weights, they were dried at 70°F for at least one day. Caloric values were measured by a Nenken type adiabatic bomb calorimeter on two samples of 1g dry weight. Caloric values were converted to calories per 1g of fresh weight.

RESULTS

For captive Ural Owls, dried pellet mass was positively correlated with the fresh weight of ingested food ($r^2 = 0.83$, $p < 0.01$). This relationship is expressed as:

1. Dried pellet mass (g) = 0.0412 x mass of ingested food (fresh weight in g).

The caloric values per gram fresh weight of the three prey species were not significantly different ($r^2 = 0.98$, $p < 0.01$). This suggests that body weight is a sufficient index of the quality of each prey species. Prey body weight was positively correlated with caloric value as follows:

2. Caloric value = 1.5762 x fresh prey body weight (g) + 0.28.

From these two linear regressions (equations 1 & 2 above) we obtained an equation for estimating caloric intake from pellet weight as follows:

3. Estimated calorie intake (kcal) = 33.82 x pellet dry weight (g) + 7.38.

We can thus estimate the food consumption of captive Ural Owls from the mass of dry pellets. The effect of owl activity and seasonal changes in energy budgets in this relationship need to be determined before applying it to Ural Owl pellets collected in the wild.

ACKNOWLEDGMENTS

We would like to thank Professor K. Ishibasi, Dr. Y. Fukuma, and Mr. H. Ito, for their helpful advice on energy analysis. We are grateful to the Niigata Prefectural Bird Protection Center for providing the owls. We would also like to thank Dr. James R. Duncan and Dr. Robert W. Nero for their encouragement and review of this manuscript.

LITERATURE CITED

Imaizumi, Y. 1968. Analysis of Ural Owl pellet contents. (In Japanese with English summary). Zool. Magazine. 77: 402-404.

Ikeda, S; Ishizawa, T. 1949. On the habits of some birds belonging to the family Strigidae. Ornithological and Mammalogical Report No.12. (In Japanese with English summary). Bureau of Agriculture and Forestry, Japan.

Matsuoka, S. 1977. Winter food habits of the Ural Owl (*Strix uralensis*) Pallas in the Tomakomai Experiment Forest of Hokkaido University. (In Japanese with English summary). Res. Bull. Coll. Exp. Forest Coll. Agric. Hokkaido Univ. 34: 161-174.

Wing Loading in 15 Species of North American Owls

David H. Johnson[1]

Abstract.—Information on wing morphology is important in understanding the mechanics and energetics of flight and in aspects related to reversed sexual size dimorphism in owls. I summarized wing span, wing area, wing loading, root box, and aspect ratio calculations from the available literature and from 113 owls examined in this study. Wing loading estimates for 15 species ranged from 0.211 to 0.545 g/cm^2. Measurements were available for both male and female owls in 12 species; males of all species had a lower wing loading. In five species with sufficient sample sizes, males had significantly lower wing loading (18 percent on average) than females of the same species. Root box area (the area between the wings) averaged 15.4 percent of the combined wing and root box areas. Aspect ratio, the ratio of the wing span to mean wing width, ranged from 4.84 to 8.90. Information is presented for the following species: Barn (*Tyto alba*), Short-eared (*Asio flammeus*), Long-eared (*A. otus*), Great Horned (*Bubo virginianus*), Barred (*Strix varia*), Great Gray (*S. nebulosa*), Northern Spotted (*S. occidentalis caurina*), Snowy (*Nyctea scandiaca*), Eastern Screech- (*Otus asio*), Western Screech- (*O. kennicottii*), Flammulated (*O. flammeolus*), Northern Pygmy- (*Glaucidium gnoma*), Northern Saw-whet (*Aegolius acadicus*), Boreal (*A. funereus*), and Burrowing (*Speotyto cunicularia*) Owls.

The type of habitat a flying or gliding animal chooses to live in, as well as its way of exploiting the habitat, are closely related to its body size, wing form, flight style, flight speed, and flight energetics. Natural selection is likely to act towards a wing structure that minimizes the power required to fly at the speed and style optimal for the animal, and is assumed to result in some near-optimal combination of these variables. The optimal flight speed varies with the flight goal and the type and abundance of food. To understand how flying animals work, their physiology, morphology, ecology, and wing function must be known.

Although there are many styles of wings, ornithologists generally recognize four basic wing types (Savile 1957). Woodpeckers, gallinaceous species, and most passerines have short, broad *elliptical wings*, designed for maneuvering through dense vegetation. Swifts, swallows, falcons, and plovers have long, narrow, slim, unslotted *high-speed wings*, designed for fast flight in open habitats. Shearwaters, albatrosses, and other seabirds have long, narrow, flat, *high-aspect-ratio wings*, designed for long-distance gliding. Last, storks, eagles, and vultures have *high-lift* or *slotted soaring wings*, which in large birds produces a very efficient soaring wing (Feduccia 1996). Most owls have relatively large, rounded, and slotted wings. Savile (1957) characterized the Eastern Screech-owl (*Otus asio*) as having a slotted high-lift wing. The "slotting" is a result of the abrupt narrowing (termed attenuation or emargination) in the distal end of up to five or six of the longest primaries. While this attenuation is limited in some owls, it is quite pronounced in others (see Averill 1927). Withers (1981) suggests that wing-tip slots have evolved because of biomechanical limitations to the bending strength of large, low-aspect ratio bird wings that could have detrimental aerodynamic consequences.

Wing loading is a metric used in determining the speed, dynamics of lift, and turning radius of birds (also bats and aircraft). It is expressed as the relationship between body mass and total wing area, calculated by dividing the weight of a bird by the surface area of both wings. Wing loading is expressed by grams per square centimeter (g/cm^2) (Clark 1971). Owls' wings are broad, with a large area in comparison to the weight of the bird, giving them a low wing-loading relative to other birds.

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Another expression of wing morphology is called aspect ratio—the ratio of wing span to mean wing width. Thus, long and narrow wings designed for high speed, have a high aspect ratio, while short, broad wings designed for low speed and maneuverability, have a low aspect ratio. In general, wing length is somewhat shorter in those bird species which hunt in cover, and longer in those which hunt in open country or are highly migratory.

The objective of this paper is to summarize the relevant literature and to provide more specific information on wing span, wing loading, root box, aspect ratio, and male/female comparisons for the owls of North America.

METHODS AND MATERIALS

Wing data for eight species was extracted from the limited literature on this topic. Data for this study was obtained from the following locations: Great Gray Owls (*Strix nebulosa*) from southern Manitoba, Boreal Owls (*Aegolius funereus*) from Idaho, a Flammulated Owl (*Otus flammeolus*) from Colorado, and nine species of owls from Oregon. With the exception of eight Great Horned Owls (*Bubo virginianus*), the owls from Oregon came from the west side of the Cascade Mountains. Except for the Northern Spotted Owls (*Strix occidentalis caurina*), Boreal Owls, and one Barred Owl (*S. varia*), all owls examined were dead. Between 1988 and 1997, over 250 owl carcasses were examined. The owls were trauma-killed, the vast majority resulting from vehicle collisions. Only fresh specimens in excellent condition were used; owls with broken wing bones, torn skin tissue, a pronounced keel suggesting cause of death by starvation, other damage, or broken or molted wing feathers were discarded. The sex of dead owls was determined through internal sexing (e.g., by looking for testes or ovaries). The sex of live Northern Spotted Owls and the Barred Owl was determined by their vocalizations and by examination for the presence/absence of a brood patch (if during the nesting season). Northern Spotted Owl wing measurements were acquired during 1988-1989 in association with other activities during a demographic study on this species. Boreal Owls were sexed by their behavior during radio-telemetry studies during the nesting season (e.g., males delivering prey to nest site; females incubating and brooding) (G. Hayward, pers. comm.). Greg Hayward (unpubl. data) submitted wing areas, weights, and capture dates for all of the Boreal Owls examined in this study. Data on a large sample of Barn Owls (*Tyto alba*) was drawn from Marti (1990); differences in his methodology should be noted. Summary wing loading and aspect ratio calculations were determined using a weighted mean, that is: (mean of males plus mean of females)/2.

Wing span—Wing span is defined as the distance (mm) from one wing tip to the other, with the wings spread horizontally as far out as they will go (fig. 1). Wing span measurements were taken with the owls placed on their backs atop a tape measure.

Wing area—Owls were held with their body facing downward and a single wing spread over a paper on a board or table (see Pennycuick 1989, p. 11). Wing area was measured by tracing around each fully extended and flattened wing. Starting where the front of the

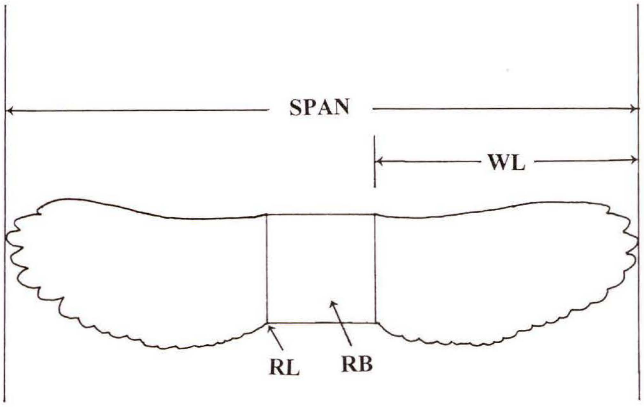

Figure 1.—*Wing span is the wingtip-to-wingtip distance (in mm), with wings spread out to the sides to their fullest extent. WL = wing length, as measured (in mm) from the wing root line to tip of the longest primary. RL = root line, a straight line depicting the interface between the wing and the owl's body. RB = root box, (in cm^2). This (reduced) tracing is from a male Western Screech-owl* (Otus kennicottii).

wing meets the body, a line was drawn following the outline of the individual feathers. After tracing the wing to where it again met the body (at the inside edge of the secondaries), the bird was lifted off the paper and a wing root line was drawn to the starting point, thus closing the wing polygon. Both wings from each owl were measured (except in Boreal Owls, where only one wing was measured). Wing tracings were digitized into a geographical information system (e.g., ArcInfo software) and the total area (cm^2) calculated. Areas of paired wings were generally within 0-3 percent of each other; the larger wing area was doubled and used in subsequent analysis. Tracing wings requires two people and some practice; the slight differences in paired wing areas were assumed to reflect differences in observer skills rather than real differences in wing areas of individual owls.

Pennycuick (1989) defines wing area differently: "*...the projected area of both wings, fully spread out, including the area of that part of the body that is included between the wing roots.*" The literature on wing loading in owls does not generally reflect Pennycuick's methodology, as the area between the wings (called the "root box") is not typically included. For this paper, I have calculated the wing area and the root box area separately. Readers wishing to follow Pennycuick's methodology will need to sum the wing area and root box area for the owls. The study by Marti (1974) was the only one I could find which included the area between the wings in wing loading calculations. Because of differences in methodology, I was not able to include data from Marti (1974) in the tables or in the analysis.

Owl weights were determined in the field with a spring scale (e.g., Pesola brand) or in the laboratory with a digital scale and recorded to the nearest gram. For dead birds, prey remains and forming pellets were removed from the stomach before weighing.

A two-tailed rank sum test was used to examine statistical differences in wing span, wing area, and wing loading between male and female owls.

Wing loading—The ratio of bird weight to the area of both wings, expressed as g/cm^2. The calculations of wing loading in this paper do not include the area of the root box.

Wing length—Wing length was determined by measuring the perpendicular distance (mm) from the wing root line to the tip of the longest primary feather (fig. 1).

Root box—The area (cm^2) between the wings (fig. 1).

Aspect ratio—The aspect ratio is a simple measure of the shape of the wing. It is the ratio of the wing span to mean wing width. Wing width is the distance from the leading edge to the trailing edge, measured along the direction of flight. The mean wing width was determined by first summing the area of both wings with the area of the root box. This summed area was then divided by the wing span. The resulting number, multiplied by 100, was the mean wing width (in mm). The wing span was then divided by the mean wing width to derive the aspect ratio.

RESULTS AND DISCUSSION

The details of wing loading calculations and related wing measurements for 15 species of owls examined in this study and/or derived from other North American studies is shown in table 1.

Table 2 reflects a simplified, composite summary of wing loading data from table 1 to allow easy comparisons with information published for owls from other countries (e.g., Mikkola 1983, p. 350). Wing loading calculations for some owls from Europe (Mikkola 1983, p. 350) and North America have strikingly similar wing loading: Great Gray Owl (0.35/0.37), Short-eared Owl (0.34/0.33), Barn Owl (0.29/0.32), and Boreal (Tengmalm's) Owl (0.29/0.28), for Europe/North America, respectively. A larger difference was seen for the Long-eared Owl (0.31/0.21) and Northern Pygmy-owl (0.26/0.35), although this difference is likely an artifact of the limited North American sample sizes.

Poole (1938) offered weight, wing area, and wing area per gram (cm^2/g—the inverse of g/cm^2) for 143 species of North American birds. After excluding the owl species, and averaging the data for species with two entries (e.g., making a single entry for males and females of the same species) from Poole's data, 132 species of birds remain. In table 3, I summarize these 132 species by range of wing loading (g/cm^2) and offer an example of a species for each

Table 1.—*Details of wing loading calculations for 15 species of North American owls. Weight, wing span, area of both wings, and wing loa data reflect mean ± one standard deviation (SD).*

Species	Sex	N	Weight (g ± SD)	Wing span (mm ± SD)	Root box (mean cm^2)	Area of both wings (cm^2 ± SD)	Wing-loading (g/cm^2)	Source
Barn Owl	male	65	473.5 ± 32.3	-	-	1576.5 ± 149.6	0.300 ± 0.030	Marti 1990
(*Tyto alba*)	female	64	566.4 ± 66.2	-	-	1663.9 ± 145.5	0.340 ± 0.030	Marti 1990
	male	1	380	1085	304.3	1394	0.273	This study
	female	6	529 ± 26.9	1133 ± 51	288.2	1691 ± 139.7	0.315 ± 0.030	This study
	unk.	2	505	-	-	1683	0.300[1]	Poole 1938
Short-eared Owl	male	2	304	-	-	1082	0.281	Clark 1975
(*Asio flammeus*)	female	2	392.5	-	-	1016	0.385	Clark 1975
Long-eared Owl	male	1	230	-	-	1182	0.195[1]	Poole 1938
(*Asio otus*)	female	2	288	-	-	1198	0.240[1]	Poole 1938
	female	2	263.7	959	241.8	1293	0.204	This study
Great Horned Owl	male	2	1106	1238	357	2264.4	0.489	This study
(*Bubo virginianus*)	female	16	1345 ± 162	1336 ± 70	412.8	2748 ± 284	0.491 ± 0.046	This study
	female	2	1446.5	-	-	2534	0.571[1]	Poole 1938
(*B. v. pacificus*)	unk.	1	1480	-	-	2426	0.610[1]	Poole 1938
Barred Owl	male	2	655	1140.5	465.3	2128	0.307	This study
(*Strix varia*)	female	2	881	1121.5	343.7	2371	0.372	This study
	unk.	1	510	-	-	1830	0.279[1]	Poole 1938
Great Gray Owl	male	5	1015 ± 178	1348 ± 40	590.0	2822 ± 140	0.349 ± 0.069	This study
(*S. nebulosa*)	female	2	1275	1413	520.7	3275 ± 28	0.390 ± 0.100	This study
Northern Spotted Owl	male[2]	12	576.5 ± 44.9	1040 ± 29	233.2	1879 ± 81	0.275 ± 0.020	This study
(*S. occidentalis caurina*)	female[2]	11	667.2 ± 47.6	1046 ± 20	228.5	1953 ± 82	0.309 ± 0.026	This study
Snowy Owl (*Nyctea scandiaca*)	male	1	1404	-	-	2576	0.545[1]	Poole 1938
Eastern Screech-owl	male	2	178	-	-	523	0.340[1]	Poole 1938
(*Otus asio*)	female	1	254	-	-	476	0.534[1]	Poole 1938
	male[3]	8	152.3 ± 11.5[4]	-	-	406.8 ± 11.0	0.326 ± 0.008	Gehlbach 1
	female[3]	8	173.9 ± 11.6[4]	-	-	463.3 ± 13.5	0.410 ± 0.012	Gehlbach 19
Western Screech-owl	male	6	153.9 ± 20.9	581 ± 28	103.8	574.6 ± 55.4	0.269 ± 0.040	This study
(*Otus kennicottii*)	female	9	201.7 ± 27.5	618 ± 26	128.7	613.6 ± 64.9	0.331 ± 0.052	This study
Flammulated Owl (*Otus flammeolus*)	unk.	1	60.2[5]	418	49.8	288.6	0.208	This study
Northern Pygmy-owl	male	1	56.4	341	49.6	163.7	0.345	This study
(*Glaucidium gnoma*)	female	4	61.5 ± 8.3	322 ± 16	36.6	171.6 ± 7.7	0.361 ± 0.063	This study
Northern Saw-whet Owl	male	1	75.0	476	63.8	404.0	0.186	This study
(*Aegolius acadicus*)	female	3	91.2 ± 3.9	502 ± 5	85.4	387.9 ± 10.9	0.235 ± 0.016	This study
	unk.	1	108	-	-	420	0.257[1]	Poole 1938
Boreal Owl	male	13	115.5 ± 6.7	-	-	485.2 ± 21.3	0.239 ± 0.017	This study
(*Aegolius funereus*)	female	12	164.8 ± 11.1	-	-	545.2 ± 36.8	0.329 ± 0.022	This study
Burrowing Owl (*Speotyto cunicularia*)	male	2	145.6	595	102.4	543.9	0.266	This study

[1] Calculated from Poole's data.

[2] Of the Northern Spotted Owls in this sample, nine males and females were mated pairs: mean weight, area of both wings, and wing loading was 576.4, 1891.0, 0.274 males and 676.1, 1966.2, 0.314 for females, respectively.

[3] These eight male and female Eastern Screech-owls were mated pairs. Except for weight, measurements are from these eight pairs.

[4] Weights from 13 males and 25 females during spring (March-June) (Gehlbach 1994, p. 66), as the specific weights for the 8 males and 8 females used in the wing loa calculations was not reported by Dr. Gehlbach.

[5] Reflects the weighted mean of 27 male and 25 female owls (Reynolds and Linkhart 1987, table 1).

Table 2.—*Summary of wing loading calculations for 15 species of North American owls.*

Species	**Wing-loading (g/cm²)**[1]	**Source**
Snowy Owl (*Nyctea scandiaca*)	0.55	Poole 1938
Great Horned Owl (*Bubo virginianus*)	0.49	Poole 1938, This study
Eastern Screech-owl (*Otus asio*)	0.38	Poole 1938, Gehlbach 1994
Great Gray Owl (*Strix nebulosa*)	0.37	This study
Northern Pygmy-owl (*Glaucidium gnoma*)	0.35	This study
Barred Owl (*Strix varia*)	0.34	This study
Short-eared Owl (*Asio flammeus*)	0.33	Clark 1975
Barn Owl (*Tyto alba*)	0.32	Marti 1990, This study
Western Screech-owl (*Otus kennicottii*)	0.30	This study
Northern Spotted Owl (*S. occidentalis caurina*)	0.29	This study
Boreal Owl (*Aegolius funereus*)	0.28	This study
Burrowing Owl (*Speotyto cunicularia*)	0.27	This study
Long-eared Owl (*Asio otus*)	0.21	Poole 1938, This study
Flammulated Owl (*Otus flammeolus*)	0.21[2]	This study
Northern Saw-whet Owl (*Aegolius acadicus*)	0.21	This study

[1] Reflects the weighted mean ((mean males + mean females)/2) only for owls where sex was known.

[2] Flammulated Owl data is based on a single individual of unknown sex.

Table 3.—*Wing loading data for 132 bird species calculated from Poole (1938). Owl species are excluded from this summary and species for which Poole had entries for both sexes have been averaged.*

Range of wing loading (g/cm²)	**Number of species**	**Example Bird Species (g/cm²)**
0.71 - 0.80	3	American Coot (*Fulica americana*) (0.73)
0.61 - 0.70	4	Dovekie (*Alle alle*) (0.66)
0.51 - 0.60	6	Turkey Vulture (*Cathartes aura*) (0.55)
0.41 - 0.50	16	Common Snipe (*Gallinago gallinago*) (0.45)
0.31 - 0.40	14	Green-backed Heron (*Butorides striatus*) (0.35)
0.21 - 0.30	34	Gray Catbird (*Dumetella carolinensis*) (0.26)
0.11 - 0.20	31	Barn Swallow (*Hirundo rustica*) (0.14)

general range. Small passerines constitute the majority of species with wing loading less than 0.31 (table 3). Many factors (e.g., flight speed, body size, diet, migration, commuting, wing shape) collectively affect wing morphology, ultimately affecting wing loading characteristics.

Data to develop aspect ratio calculations was available for 13 species of owls. The aspect ratio for the owls examined in this study ranged from 4.84 to 8.90 (table 4). Species having the highest aspect ratio (long wing span relative to wing width) were the Short-eared, Barn, and Long-eared owls. This is not surprising as these owls hunt in the open while flying and regularly move over great distances. Those with the lowest aspect ratio (short wing span relative to wing width) were the Barred, Spotted, Northern Saw-whet, and Western Screech-owl. These species are sit-and-pounce hunters that spend their time in closed-canopy forests, often with very dense vegetation.

Root box areas were determined for 11 species (table 1) and averaged 15.4 percent of the combined wing and root box areas. For the

Table 4.—*Aspect ratio calculations for 13 species of North American owls.*

Species	Sample	Aspect ratio
Short-eared Owl (*Asio flammeus*)	2 males/2 females	8.90[1]
Barn Owl (*Tyto alba*)	1 male/6 females	6.72
Long-eared Owl (*Asio otus*)	2 females	6.00
Great Horned Owl (*Bubo virginianus*)	2 males /16 females	5.77
Eastern Screech-owl (*Otus asio naevius*)	1 unk.	5.50[2]
Burrowing Owl (*Speotyto cunicularia*)	2 males	5.50
Great Gray Owl (*Strix nebulosa*)	5 males/2 females	5.31
Northern Pygmy-owl (*Glaucidium gnoma*)	1male /4 females	5.22
Flammulated Owl *(Otus flammeolus*)	1 unk.	5.16
Northern Spotted Owl *(Strix occidentalis caurina*)	12 males /13 females	5.10
Northern Saw-whet Owl (*Aegolius acadicus*)	1 male /3 females	5.09
Western Screech-owl (*Otus kennicottii*)	6 males /9 females	5.08
Barred Owl (*Strix varia*)	2 males/2 females	4.84

[1] Clark 1975.
[2] Savile 1957.

most part, this percentage was relatively consistent among the owls (root box area was between 14.5 - 16.0 percent in eight species). The percentage of combined area in the root box was the smallest in Northern Spotted Owls (10.5 percent) followed by Great Horned Owls (13.3 percent), and largest in the Northern Pygmy-owl (20.5 percent).

An important aspect in flight is that of drag, some of which is generated from the body and some from its wings. The body diameter for two owl species was recorded by comfortably (feathers not compressed) wrapping a string around the owls, just behind the wings, and the length of the string measured to acquire the circumference. The diameter was then calculated. The diameter for one female Northern Saw-whet Owl was 64.7 mm; average for two male Great Horned Owls was 123 mm; average for four female Great Horned Owls was 133 mm.

Comparisons Between Males and Females

Wing span data was available for males and females of eight species (table 1). Barred Owl and Northern Pygmy-owl males had longer wing spans than females of these species. Female Barn, Great Horned, Great Gray, Spotted, Western Screech-owl, and Northern Saw-whet Owls had longer wing spans than males of these species. Sample sizes allowed statistical examination for two species. Female Western Screech-owls had significantly longer wing spans than males (P = 0.01). Northern Spotted Owl females had only slightly longer wing spans (6 mm on average) than males, and the difference was not significant (P = 0.41).

Wing area data was available for males and females of 12 species (table 1). While wing areas for male Short-eared and Northern Saw-whet Owls were larger than for females of these species, wing areas of female Barn, Long-eared, Great Horned, Barred, Great Gray, Northern Spotted, Eastern Screech-, Western Screech-, Northern Pygmy-, and Boreal Owls were larger than the males of these species. Sample sizes allowed statistical examination for five species (Barn, Spotted, Eastern Screech-, Western Screech-, and Boreal Owls). Wing areas were significantly larger in female Barn (P = 0.0005, Marti 1990), Northern Spotted (P = 0.04), Eastern Screech- (P < 0.001, Gehlbach 1994, p. 257), and Boreal owls (P < 0.001) than in males of the same species. While wing areas in female Western Screech-owls were larger than in males, the difference was not significant (P = 0.22). Great Gray Owls had the largest wing area of any of the owl species, and it was interesting that female Great Grays had wing areas 14 percent larger than males of this species.

Wing loading data was available for males and females of 12 species. Males of all species had lighter wing loading than females (table 1).

Sample sizes allowed statistical examination for five species (Barn, Northern Spotted, Eastern Screech-, Western Screech-, and Boreal Owls). For all five species, males had significantly lower wing loading than females of the same species; Barn ($P < 0.0001$, Marti 1990), Northern Spotted ($P = 0.002$), Eastern Screech- ($P = 0.01$, Gehlbach 1994, p. 71), Western Screech- ($P = 0.027$), and Boreal ($P < 0.001$) Owls. On average, wing loading was 18 percent (range 11.0-27.4 percent) lower in males for these five species.

Depending on the season, owl weights can change substantially, thus affecting wing loading calculations (McGillivray 1987). Seasonal weight changes in the Eastern Screech-owl reflected a total weight loss of 19 percent (Gehlbach 1994, p. 257), and 24 percent in Great Gray Owls (J. Duncan, unpubl. data). One nesting Great Gray Owl female went from 1,600 g in March to 1,000 g in July, a 37.5 percent decrease in weight (J. Duncan, pers. comm.). These changes are similar to the 15.2 ± 4.1 percent reported by Korpimäki (1990) for five species of breeding raptors including the Boreal, Little (*Athene noctua*), and Tawny (*Strix aluco*) Owls, and the 25 percent change in female Long-eared Owls (Wijnandts 1984). Seasonal weight differences of male and female owls is clearly an important aspect in wing loading and flight mechanics in owls. Sample sizes for some owls in this study were very small, and in general, are difficult to acquire. Additional owl weight information was summarized by Dunning (1985) and readers are referred to that work.

One particular Northern Spotted Owl (a female) examined in this study, had been captured and weighed seven times over a 12-year period. When first captured in 1976, she was 12 months old, and had just become established on a territory. Weights were acquired during the months of May, June, and August (the breeding season; she nested in only 2 of the years in which she was weighed). Her average weight was 683 g (range 605-733 g; a variation of ±13 percent from the mean). Assuming that her wing area remained relatively constant at 1,993 cm^2, her "average" wing loading was 0.343 g/cm^2 (range 0.304-0.368). Whether the change in weight was significant is debatable: (1) at 14 years, she was one of the oldest known Northern Spotted Owls living in the wild, (2) she seldom nested, possibly suggesting that she was in poor physical condition. Deteriorating habitat conditions within her consistently-held territory may have been a factor in her poor condition.

Andersson and Norberg (1981) noted that size affects the flight performance of birds, particularly in pursuit of prey, and suggested that this might be an important factor in the evolution of reversed sexual size dimorphism (RSD). Schantz and Nilsson (1981) believed that an important factor in the evolution of RSD is the relative ability to transport large prey. These aspects of flight are greatly influenced by wing loading. Mueller (1986) developed an index for wing loading, obtained by dividing weight by the square of "wing length" (actually the wrist-to-tip measurement). While a reasonable attempt, the index underestimated the differences in wing loading between male and female owls; differences found in this study were about twice that as determined by Mueller's index.

The aspect ratio for the owls examined in this study ranged from 4.84 to 8.90. In a review of 141 bird species, Norberg (1990, p. 239) noted that the aspect ratio ranged from 4.4 to 17.2. For comparison, the Gray Catbird's (*Dumetella carolinensis*) aspect ratio is 4.7 (Savile 1957), and that of *Archaeopteryx* is 7.0 (Norberg 1990, p. 243). In two species of albatross, where wing span greatly exceeds wing width, aspect ratios of 15 and 18 have been calculated.

Since flight is expensive, there should be strong selection to minimize the mechanical power required to fly. Low total power is attainable with a high aspect ratio, particularly when this is combined with a low body mass and low wing loading. Migratory species should have wings of high aspect ratio for enduring flight (Pennycuick 1975). Flying within vegetation puts demands on slow flight and short wings that have to be broad to compensate for their shortness and give enough area to allow slow flight. Slow flight and tight turning radius are achieved by a low wing loading (Norberg 1990). Species taking heavy prey should have a large wing area (low wing loading) so that they can carry the extra weight. The combination of aspect ratio and wing loading can reveal patterns which aid in understanding the relationship between wing shape, flight behavior, and foraging strategies in the owls (as well as in other birds and bats).

In this paper, "wing width" is the same measurement as "wing chord" (see Norberg 1987, Pennycuick 1989, p. 13). Some ornithologists use the term "chord" to refer to the distance from wrist to wing tip of the folded wing. As noted by Pennycuick (1989), the wrist-to-tip measurement is not the chord, and should be given a different name, such as "wrist-to-tip distance" or "folded wing length". The "wrist-to-tip distance" or "folded wing length" does not have any straightforward significance for flight mechanics. Mass, along with wing span, are measurements necessary for calculations of powered flight. Biologists are encouraged to record and report wing span, weights, and wing area information in conjunction with other efforts involving the handling of owls.

Cautionary note.—Sample sizes for many owl species in this study are quite small. As additional sample sizes are obtained, general and statistical comparisons of wing loading and other aspects of wing measurements will be substantially improved. In this study, sample sizes of 10 or more appeared sufficient to capture the majority of the variability in owl wing measurements.

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LITERATURE CITED

Andersson, M.; Norberg, R.A. 1981. Evolution of reversed sexual size dimorphism and role partitioning among predatory birds, with a size scaling of flight performance. Biological Journal of the Linnean Society. 15: 105-130.

Averill, C.K. 1927. Emargination of the long primaries in relation to power of flight and migration. Condor. 29: 17-18.

Clark, R.J. 1971. Wing loading—a plea for consistency in usage. Auk. 88: 927-928.

Clark, R.J. 1975. A field study of the Short-eared Owl *Asio flammeus* (Pontoppidan) in North America. Wildlife Society Monograph. 47. 67 p.

Dunning, J.B., Jr. 1985. Owl weights in the literature: a review. Raptor Research. 19(4): 113-121.

Feduccia, A. 1996. The origin and evolution of birds. Yale University Press. 420 p.

Gehlbach, F.R. 1994. The Eastern Screech-owl: life history, ecology, and behavior in the suburbs and countryside. Texas A&M University Press. 302 p.

Korpimäki, E. 1990. Body mass of breeding Tengmalm's Owl (*Aegolius funereus*): seasonal, between-year, site, and age-related variation. Ornis Scandinavica. 21: 169-178.

Marti, C.D. 1974. Feeding ecology of four sympatric owls. Condor. 76: 45-61.

Marti, C.D. 1990. Sex and age dimorphism in the Barn Owl and a test of mate choice. Auk. 107: 246-254.

McGillivray, W.B. 1987. Reversed size dimorphism in 10 species of northern owls. In: Nero, R.W.; Clark, R.J.; Knapton, R.J.; Hamre, R.H., eds. Biology and conservation of northern forest owls: symposium proceedings; 1987 February 3-7; Winnipeg, Manitoba. Gen. Tech. Rep. RM- 142. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 56-66.

Mikkola, H. 1983. Owls of Europe. Buteo Books. 397 p.

Mueller, H.C. 1986. The evolution of reversed sexual dimorphism in owls: an empirical analysis of possible selective factors. Wilson Bulletin. 98(3): 387-406.

Norberg, R.A. 1987. Evolution, structure, and ecology of northern forest owls. In: Nero, R.W.; Clark, R.J.; Knapton, R.J.; Hamre, R.H., eds. Biology and conservation of northern forest owls: symposium proceedings; 1987 February 3-7; Winnipeg, Manitoba. Gen. Tech. Rep. RM-142. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 9-43.

Norberg, U.M. 1990. Vertebrate flight. New York, NY: Springer-Verlag. 291 p.

Pennycuick, C.J. 1975. Mechanics of flight. In: Farner, D.S.; King, J.R., eds. Avian biology, vol 5. New York, NY: Academic Press: 1-75.

Pennycuick, C.J. 1989. Bird flight performance: a practical calculation manual. Oxford University Press. 153 p.

Poole, E.L. 1938. Weights and wing areas in North American birds. Auk. 55: 511-517.

Reynolds, R.T.; Linkhart, B.D. 1987. The nesting biology of Flammulated Owls in Colorado. In: Nero, R.W.; Clark, R.J.; Knapton, R.J.; Hamre, R.H., eds. Biology and conservation of northern forest owls: symposium proceedings; 1987 February 3-7; Winnipeg, Manitoba. Gen. Tech. Rep. RM-142. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 239-248.

Savile, D.B.O. 1957. Adaptive radiation of the avian wing. Evolution. 11: 212-224.

Schantz, T. Von; Nilsson, I.N. 1981. The reversed size dimorphism in birds of prey: a new hypothesis. Oikos. 36: 129-132.

Wijnandts, H. 1984. Ecological energetics of the Long-eared Owl (*Asio otus*). Ardea. 72: 1-92.

Withers, P.C. 1981. The aerodynamic performance of the wing in Red-shouldered Hawk (*Buteo linearis*) and a possible aeroelastic role of wing-tip slots. Ibis. 123: 239-247.

Preliminary Investigation of Vocal Variation in the Mexican Spotted Owl (*Strix occidentalis lucida*): Would Vocal Analysis of the Four-note Location Call be a Useful Field Tool for Individual Identification?

Wendy A. Kuntz and Peter B. Stacey[1]

Abstract.—Individual identification, especially in rare species, can provide managers with critical information about demographic processes. Traditionally, banding has been the only effective method of marking individuals. However, banding's drawbacks have led some researchers to suggest vocal analysis as an alternative. We explore this prospect for Mexican Spotted Owls (*Strix occidentalis lucida*) using a visual examination of the male four-note location call. While there appears to be a low level of within-individual variation, preliminary investigation suggests there is enough pattern overlap between different owls to caution against using visual examination of vocalizations as a field method to identify individuals.

Many species of birds, including some owls, have been shown to exhibit individual variation in their songs and calls (Appleby and Redpath 1997, Catchpole and Slater 1995, Falls 1982, Otter 1996). This variation suggests that owls might use vocalizations to recognize not only conspecifics, but individual neighbors (Falls 1982). If birds are using vocalizations to recognize each other, might it not be possible for humans to use the same cues to identify specific individuals? In the past, identifying individual birds has usually required banding, but if the level of inter-individual variation in a species song or call is high, it presents the possibility that vocalizations could provide an alternative method for recognizing individuals. This is especially appealing for birds which are widely dispersed and difficult to locate, like many threatened or endangered species, including the Mexican Spotted Owl (*Strix occidentalis lucida*).

Banding programs require properly supervised personnel who are trained in safe capture techniques. Field crews must often spend long days to locate owls at roost sites or use traps to capture owls at night, each of which demands extensive field time. For example, it has been estimated that marking individual Mexican Spotted Owls for population estimates may increase the costs of management and recovery by up to 40 percent (USDI 1995). In contrast, tape recording owl vocalizations could be relatively inexpensive and therefore cost effective. Most owl surveys already incorporate the use of broadcast calling to locate individuals, and it is currently a major census technique for the Mexican Spotted Owl (USDI 1995). This provides an opportunity for field crews to tape record owl responses as part of their standard survey procedure.

We decided to explore the feasibility of a vocal identification method for Mexican Spotted Owls using tape recordings we had collected in 1995 and 1996 as part of a larger study on vocal dialects and genetic structure. Individual identification through call type has recently been suggested for some other owl species, both informally at the agency level and in recent literature (e.g., Galeotti *et al.* 1993, Otter 1996). However, the accuracy and efficiency of vocal analysis as a management tool is still debatable. It was not found to be a reliable field marker in studies of Bald Eagles (*Haliaetus leucocephalus*) (Eakle *et al.* 1989). The dependability of vocal analysis may vary with the species and with the methods used for analysis (Gilbert *et al.* 1994).

Recorded vocalizations can be used as a tool for identifying individuals by generating a pictorial display of the call as a spectrograph. In the

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past, the generation of spectrographs required special equipment, but it is now possible to use a personal computer to create equivalent displays, not only in the lab, but also potentially in the field with a portable computer (for example with the CANARY software program produced by the Cornell Lab of Ornithology, Ithaca, NY).

Spectrographs can be analyzed either through a straightforward visual examination, or by the more time consuming technique of quantifying time and frequency variables to establish individual differences using statistical methods (e.g., Appleby and Redpath 1997, Otter 1996). Because analysis of spectrographs using time and frequency variables is much more complex and labor intensive, we believe that visual examination is at present the only efficient field technique for identifying individuals. While it may be theoretically possible to write a computer program based on quantitative statistical analysis, in a practical sense this would still be beyond the capabilities of most field projects. Our objective in this analysis was to determine if a visual examination could reliably identify individuals and/or distinguish among populations. We hope this preliminary study provides managers with some insight into the possible use of vocalizations to identify individual Spotted Owls in the field.

METHODS

We tape recorded male Mexican Spotted Owls in five mountain ranges in New Mexico during the spring and summer (breeding season) of 1995 and 1996. The male four-note location call is the most commonly heard call and the most frequently recorded (Ganey 1990). Females also give four-note location calls, but much less frequently and they do not engage in long calling bouts. Males generally give 1 to 2 four-note location calls per night. We recorded spontaneous four-note calls but, if none occurred, we then solicited calls from the males using playback. Vocalizations were recorded using a PMD 221 Marantz Recorder, a Sennheiser microphone and a 56 cm (22 inch) fiberglass parabola. Most of the owls recorded were also banded with U.S. FWS band on one leg and one color band on the other leg for individual identification. For owls that remained unbanded only one season of recording per territory was used in the analysis. We determined the sex of an owl by observing size and behavior. Males are generally smaller and have a lower frequency vocalization (see Forsman 1983). Owl calls were digitized and displayed as spectrographs using a Macintosh computer in the laboratory.

RESULTS

We examined six spectrographs each from two males (San Mateo male #29786 and Zuni male #77366) which were chosen because both were recorded on several occasions, both within and between years (figs. 1 and 2). Each set of six spectrographs included samples from three separate recording sessions, two from 1995 and one from 1996. Establishing a low level of intra-individual variation is an essential prerequisite for any method of inter-individual identification. Visual inspection shows there is a striking consistency in note shape and structure over time for both males, but there is variation in the spacing or timing of individual notes (figs. 1 and 2). The consistency of note shape and structure for these two males suggests that owls may retain an individual call type within and between seasons.

We then visually inspected spectrographs from a total of 21 male Mexican Spotted Owls to determine the feasibility of identifying individuals and/or populations by call. These included the Zuni Range in northwestern New Mexico (n = 5), the Black Range in southwestern New Mexico (n = 6), the San Mateo Range in southwestern New Mexico (n = 7), the Magdalena Range in southwestern New Mexico (n = 1), and the Jemez Mountains in north central New Mexico (n = 2). We then chose the first quality recordings of each male (n = 2-6) and examined them for unique and/or identifying characteristics. We assessed visual similarities among the spectrographs in note shape and call structure. While many calls show unique traits which might potentially serve as identifying characters, there were some calls that showed marked similarities. One of the most notable overlaps can be seen in spectrographs from two males in the adjoining Upper and Lower Hoyt Canyon territories in the Black Range (fig. 3).

We also grouped calls by mountain range. Cursory visual inspection revealed that the greatest variation in note shape and structure occurred in the third note of the four-note call. We assigned three descriptive types: type A, a single-peak note, type B, a double-peak note, and type C, an intermediate note shape. Three

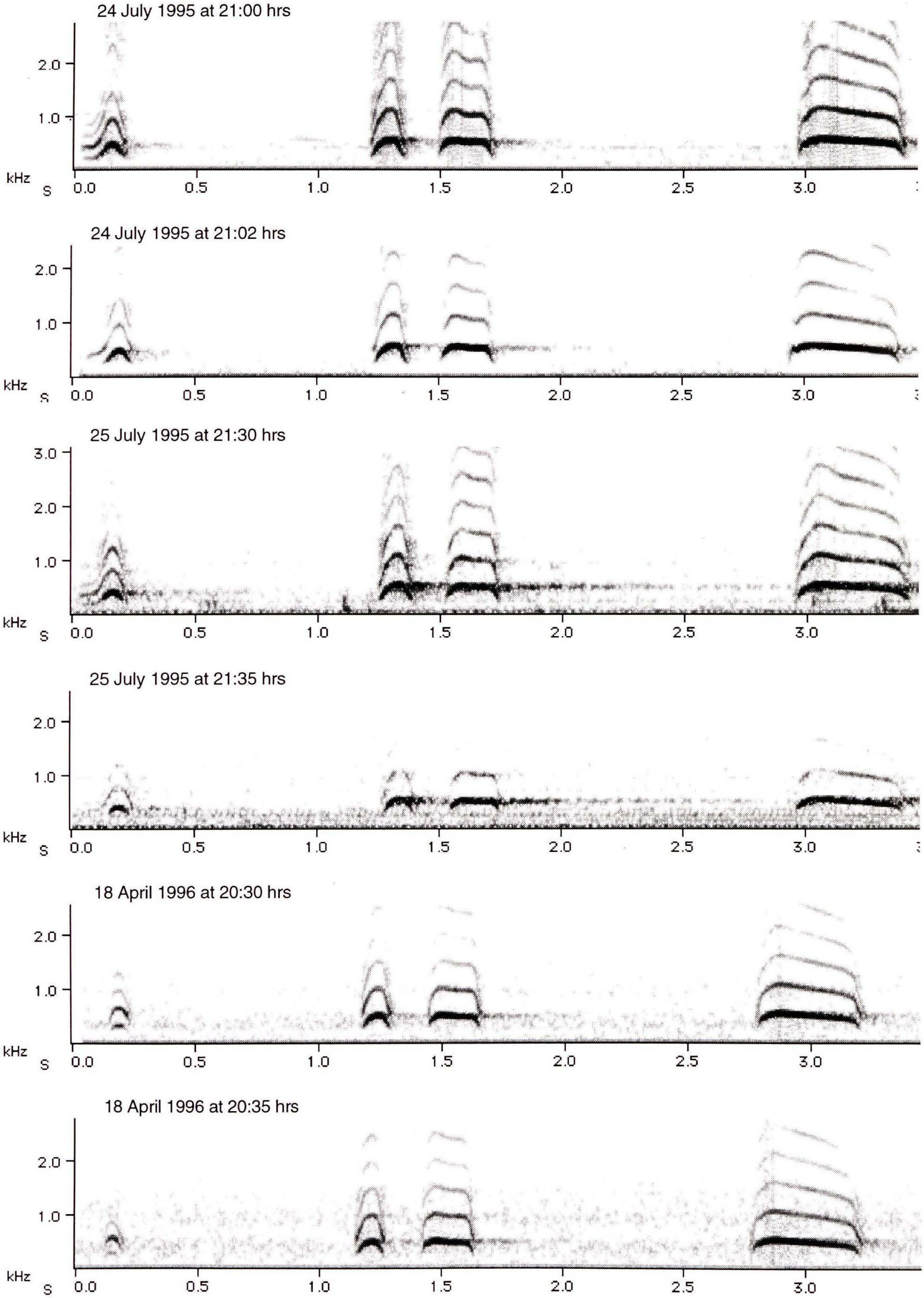
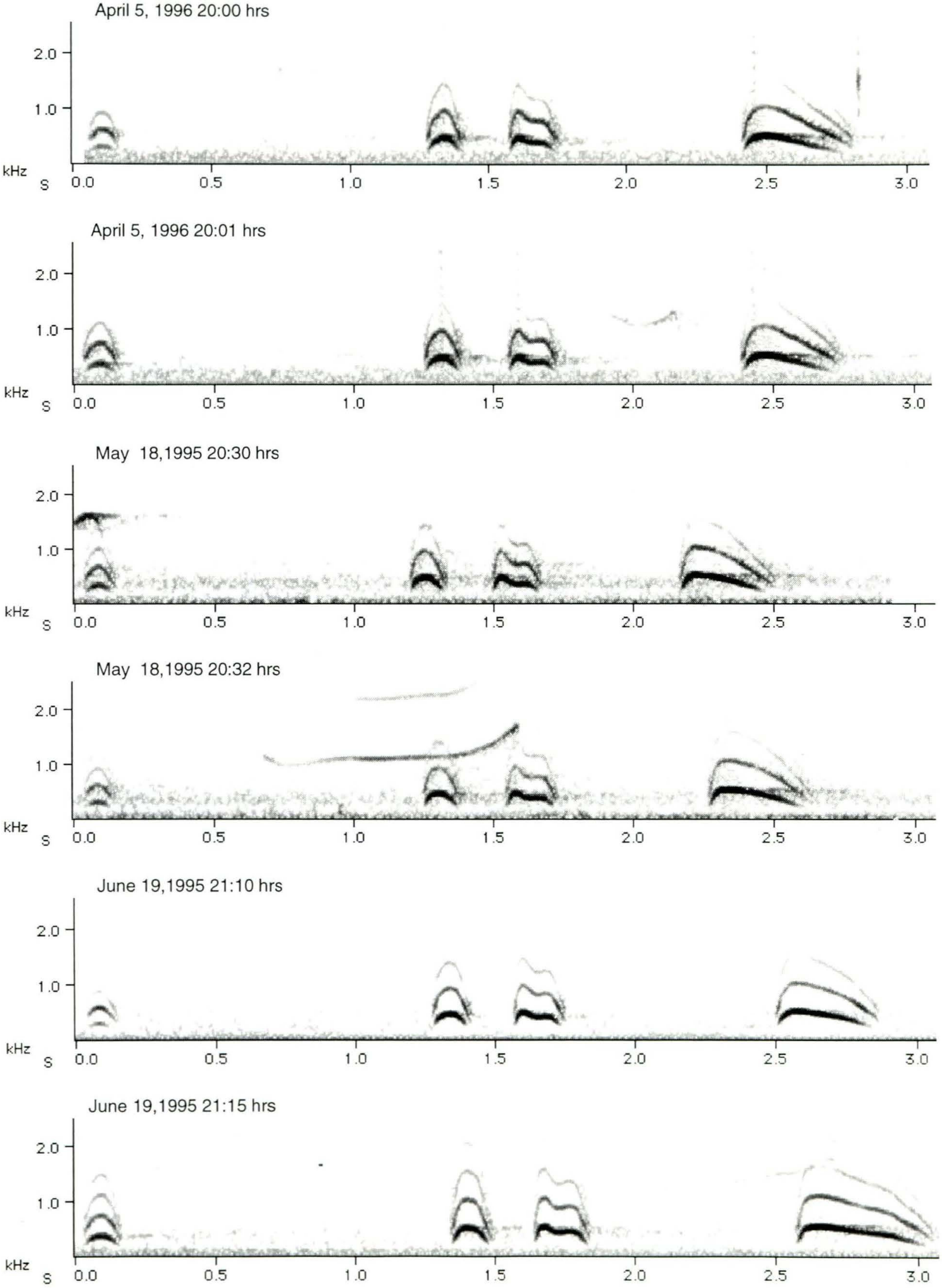
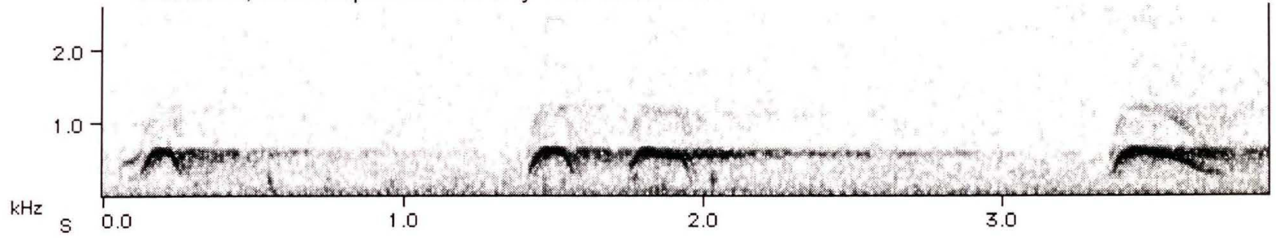


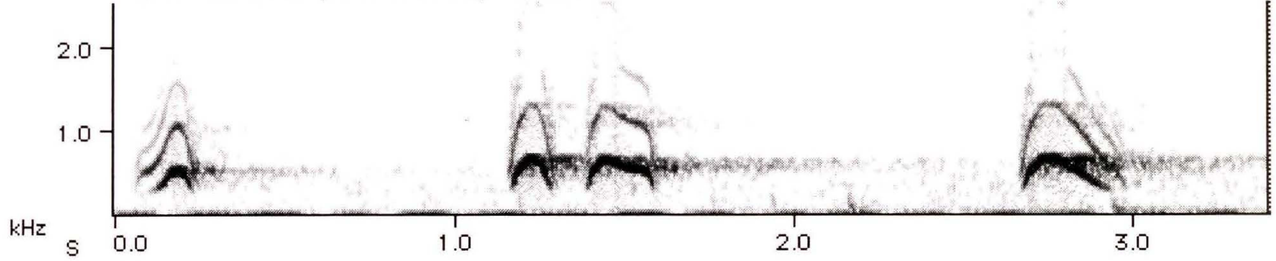
Figure 1.—*Sample spectrographs from one male Mexican Spotted Owl (*Strix occidentalis lucida*), San Mateo #29786. Spectrographs are taken from three separate recording sessions in 1995 and 1996 in New Mexico. Time in seconds is represented on the x-axis and frequency in kHz is represented on the y-axis. Note both the consistency in note shape and structure over different recording sessions and the variation in note timing, or spacing.*



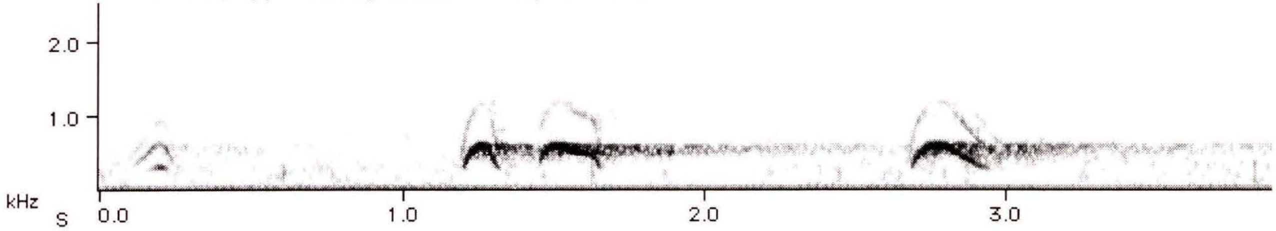
*e 2.—Sample spectrographs from one male Mexican Spotted Owl (*Strix occidentalis lucida*), Zuni #77366. Spectrographs are taken from hree separate recording sessions in 1995 and 1996 in New Mexico. Time in seconds is represented on the x-axis and frequency in kHz is epresented on the y-axis. Note both the consistency in note shape and structure over different recording sessions and the variation in note ming, or spacing. The shape and structure of the third note is seen in the Zuni population, but not in the other mountain ranges. The long orizontal portions are overlapping whistle calls given by the mated female which was present and vocalizing at the same time.*



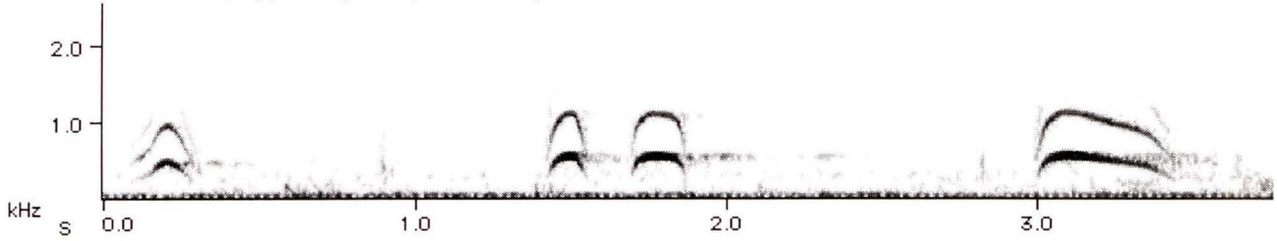
Unbanded, Aldo Leopold #5. 23 July 1996 at 23:20 hrs



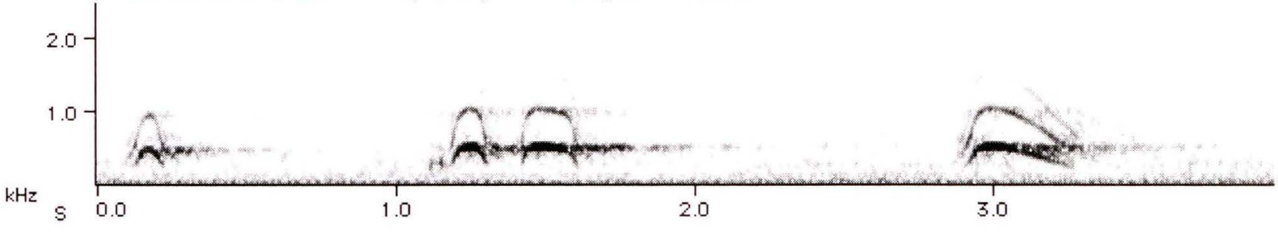
#52119 Aldo Leopold #2. 14 May at 23:00 hrs



#52122, Upper Turkey Creek. 07 July 1996 at 21:40 hrs



#49924, Upper Hoyt Canyon. 16 July at 22:30 hrs



Unbanded male, Lower Hoyt Canyon. 17 July at 21:30 hrs

Figure 3.—*Sample spectrographs from five male Mexican Spotted Owls* (Strix occidentalis lucida), *from the Black Range, New Mexico. One spectrograph per individual is given. Time in seconds is represented on the x-axis and frequency in kHz is represented on the y-axis. Note the similarity in note shape and structure between #49924, Upper Hoyt Canyon, and the Unbanded male from the adjacent territory, Lower Hoyt Canyon.*

of the five males recorded in the Zuni Mountains possessed the type B, or double-peak note (table 1). Zuni male #77366, shown in figure 2, displays this type B structure in the third note. None of the owls in the other four mountain ranges exhibited this type of call. Males from the remaining four mountain ranges overwhelmingly possessed the type A, or single-peak note (15 of 16 observations). One intermediate, or type C note, was observed in the Black Range male #52119, Aldo Leopold #2 (shown in fig. 3) .

Table 1.—*Occurrence of type A (a single-peak note), type B (a double-peak note), and type C (an intermediate note shape) from Mexican Spotted Owls (*Strix occidentalis lucida*) in New Mexico mountain ranges.*

Range	Type A	Type B	Type C
Zuni (5)	2	3	-
Black (6)	5	-	1
San Mateo (7)	7	-	-
Magdalena (1)	1	-	-
Jemez (2)	2	-	-

DISCUSSION

For researchers working on threatened or endangered species a new, and potentially less invasive technique for identifying individuals holds great appeal. Thanks to the recent portability of personal computers, field biologists now possess the ability to rapidly digitize vocalizations and include spectrographs as part of their field tools. For this process to be an effective field method, individuals should be readily identifiable from spectrographs without lengthy and time consuming statistical analyses.

Our examination of four-note calls for two individuals (San Mateo #29786 and Zuni #77366) suggests that there was a fairly low level of intra-individual variation in note shape and structure. However, differences in the spacing or timing of notes were evident (figs. 1 and 2). This variation in timing could be a recording artifact (due to battery power or tape quality), but more likely it reflects the level of excitement of an owl at a particular recording time, resulting in a speeding up, or slowing down, of the pacing of the four-notes. Eakle *et al.* (1989) noted a similar problem in recordings of Bald Eagle calls and related it to changes in motivation. This suggests that individual identification of Mexican Spotted Owls by call cannot be based on spacing differences and may need to depend solely on note shape and structure.

Our preliminary examination of two male owls suggests that individuals do maintain note shape and structure over time. However, is there enough variation between birds to reliably identify individuals from a visual inspection of spectrographs? We looked at spectrographs of four-note calls from 21 male Mexican Spotted Owls and found that while some owls appear to posses unique and identifying notes, there were several individual males with strikingly similar calls. The visual similarity among some four-note calls points out a major problem for discriminating individual owls using spectrographs. It is unlikely that visual cues alone could separate all males with accuracy. Although a quantitative analysis may reveal differences between individuals, it is not likely to provide a suitable field method at least for the immediate future.

Even if individuals living in the same mountain range cannot always be identified, vocalizations may provide an index for delimiting some populations. Interestingly, the most northern and physically distant population in our sample, the Zuni Mountains, had three out of five individuals with a rare double-peak (B type) structure in the third note. This implies that there is some level of vocal divergence among populations. Since all individuals with the type B note could be categorized as part of the Zuni population, the type B note may serve as a population-specific marker. The Zuni mountain populations, however, also contained the type A note and therefore may present a transition zone between two note types. Further research on owl call shape and structure within this geographic area is needed.

CONCLUSIONS

At this time, we believe that the field utility of vocal analysis to identify individual owls depends on a method that can assess call variations using a visual examination of the spectrograph. Our preliminary investigation, however, suggests that there may be too much overlap in the calls of certain owls to reliably identify individuals. We agree that expanded quantitative analysis could possibly illuminate differences which are not readily identifiable by eye and we are currently conducting such an analysis which utilizes time and frequency variables. In the future, computer programs may provide field crews easy access to complex analyses, but at present, for most field projects this is not a realistic option.

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LITERATURE CITED

Appleby, B.M.; Redpath, S.M. 1997. Variation in the male territorial hoot of the Tawny Owl (*Strix aluco*) in three English populations. Ibis. 139: 152-158.

Catchpole, C.K.; Slater, P.J.B. 1995. Bird song: biological themes and variations. London, England; Cambridge University Press.

Eakle, W.L.; Mannan, R.W.; Grubb, T.G. 1989. Identification of individual breeding Bald Eagles by voice analysis. Journal of Wildlife Management. 53: 450-455.

Falls, J.B. 1982. Individual recognition by sound in birds. In: Kroodsma, D.E.; Miller, E.H., eds. Acoustic communication in birds: Vol. 2. New York, NY; Academic Press: 237-278.

Forsman, E.D. 1983. Methods and material for locating and studying Spotted Owls. Gen. Tech. Rep. PNW-162. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 8 p.

Galeotti, P.; McGregor, P.K.; Tyler, G. 1993. Individually distinct hooting in male Pygmy Owls *Glaucidium passerinum*: a multivariate approach. Ornis Scandinavia. 24: 15-20.

Ganey, J. 1990. Calling behavior of Spotted Owls in northern Arizona. The Condor. 92: 485-490.

Gilbert, G.; McGregor, P.K.; Tyler, G. 1994. Vocal individuality as a census tool: practical considerations illustrated by a study of two species. Journal of Field Ornithology. 65: 335-348.

Otter, K. 1996. Individual variation in the advertising call of Northern Saw-whet Owls. Journal of Field Ornithology. 67: 398-405.

USDI Fish and Wildlife Service. 1995. Recovery plan for the Mexican Spotted Owl: Vol. 1. Albuquerque, NM: U.S. Department of the Interior, Fish and Wildlife Service, Southwestern Region. 172 p.

Range Expansion of Northern Hawk Owls (*Surnia ulula*) and Boreal Owls (*Aegolius funereus*) in Nova Scotia

Randy F. Lauff[1]

Abstract.—The Northern Hawk Owl (*Surnia ulula*) has never been recorded to breed in Nova Scotia (and only once in recent history in all of the Maritimes). Three pairs of hawk owls were found within 4 km² of woods in 1996, and of these, young were found with two pairs. The first provincial summer record for the Boreal Owl (*Aegolius funereus*) was also obtained in 1996. These findings increase the known breeding range of hawk owls (and likely that of Boreal Owls) to the south and east of that previously described in North America. The range extension of the hawk owl may be explained by a beneficial habitat change which resulted from a major outbreak of the spruce budworm (*Choristoneura fumiferana* (Clemens)).

A major outbreak of the spruce budworm (*Choristoneura fumiferana*) caused total defoliation and death of most softwood trees in and around Cape Breton Highlands National Park during the late 1970s and early 1980s. The only large trees left alive in the study area were white birch (*Betula papyrifera*). Since then, a lush understory developed allowing for the existence of dense populations of small mammals. The Northern Hawk Owl (*Surnia ulula*) is classified as a rare winter visitor in Nova Scotia (Tufts 1986). The Boreal Owl (*Aegolius funereus*) also is without breeding records for the province. The purpose of our expedition was to document the presence of a number of rare animals and plants, including the two owls. Figure 1 indicates the location of the study site in Nova Scotia, as well as the Canadian breeding distribution for the Northern Hawk Owl and Boreal Owl.

METHODS

We searched for Northern Hawk Owls during daylight hours anytime we were in appropriate habitat. Boreal Owls were sought in the early evening by either playing a tape or imitating their breeding call. Another goal of the expedition was to locate disjunct populations of two small mammals, arctic shrew (*Sorex arcticus* (Kerr)) and northern bog lemming (*Synaptomys borealis* (Richardson)). We did this by laying out snap traps (baited with peanut butter and rolled oats) to give us an indication of the relative density of the small mammals that were potential prey for the owls. Trap line transects were placed randomly to cover the largest representative area. Lines were 90 m long and consisted of one snap trap set every 10 m. Traps were placed for an average of 4 nights per trap line.

RESULTS AND DISCUSSION

Although we did not find either of the target small mammal species, we did capture five other species of small mammals. Trapping success was 19.6 percent (36 animals, 184 trap-nights). This trapping success represents a very high relative density of small mammals and is undoubtedly responsible for the numerous predators (mostly avian) that we encountered. The number of each species trapped is as follows: 16 *Microtus pennsylvanicus* (Ord), 15 *Clethrionomys gapperi* (Vigors), 3 *Napaeozapus insignis* (Miller), 1 *Sorex cinereus* (Kerr), and 1 *S. fumeus* (Miller).

We found three pairs of Northern Hawk Owls (fig. 2) in approximately 4 km² of forest; two of these pairs had young (figs. 3, 4). In addition to the Hawk Owls, we also found Great Horned Owls (*Bubo virginianus*), American Kestrels (*Falco sparverius*), Red-tailed Hawks (*Buteo jamaicensis*), and one Boreal Owl (fig. 5). The presence of the Red-tailed Hawk alludes to the openness of the woods (fig. 6).

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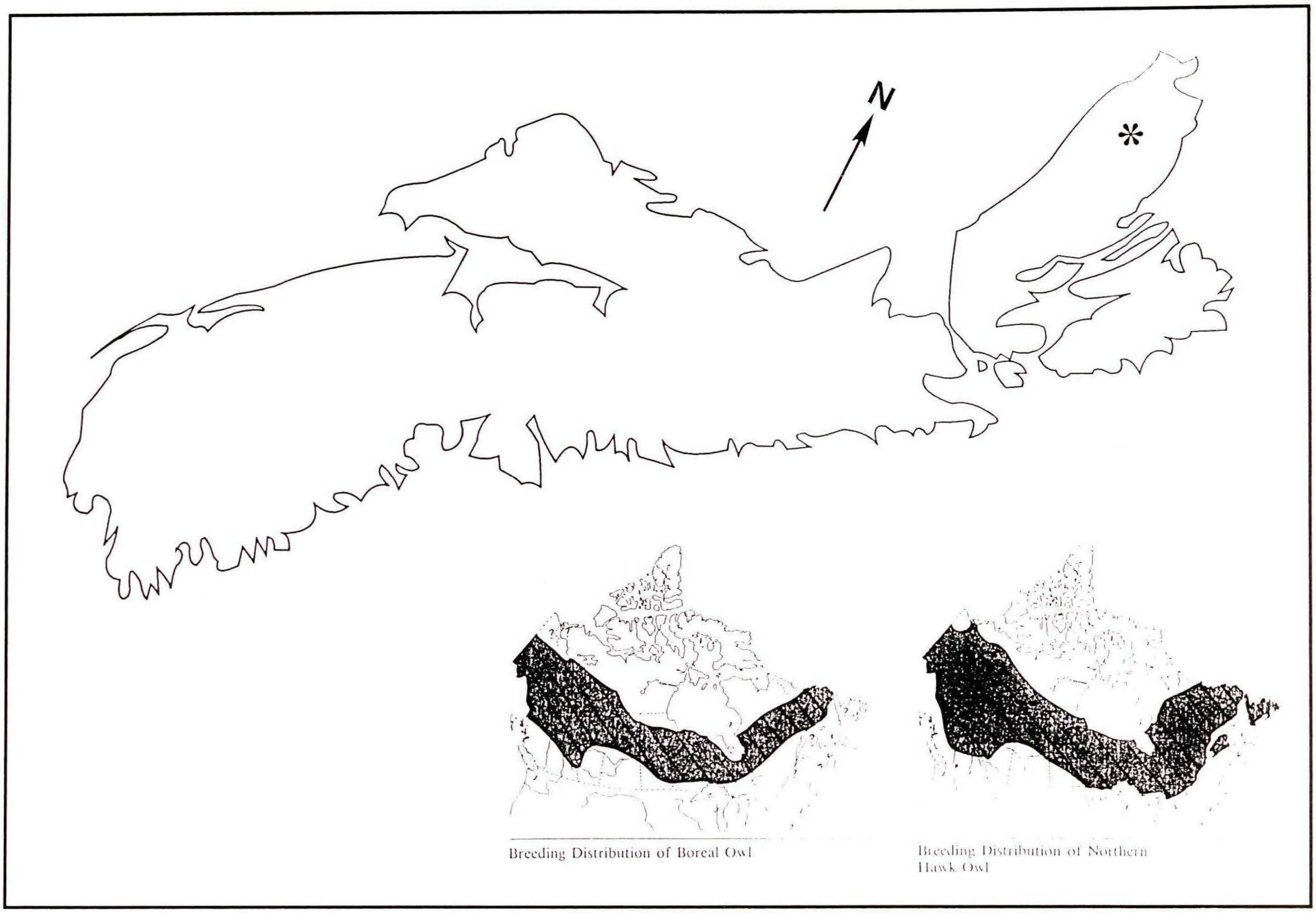
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Breeding Distribution of Boreal Owl
Breeding Distribution of Northern Hawk Owl

Figure 1.—*Canadian breeding distribution (Godfrey 1986 and courtesy of the Canadian Museum of Nature, Ottawa) for both owls and the study site (*) in Nova Scotia where the new records were documented. (W.E. Godfrey,* The Birds of Canada, 1986. *Courtesy of the Canadian Museum of Nature, Ottawa.)*

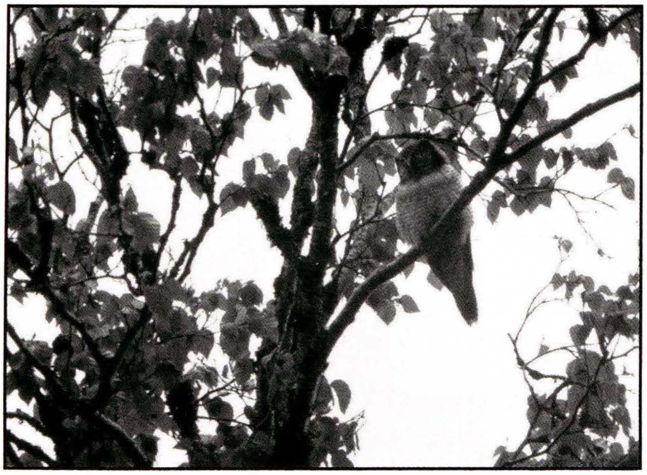

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Figure 2.—*Adult Northern Hawk Owl (*Surnia ulula*) near the nest site (June 1996), Nova Scotia, Canada.*

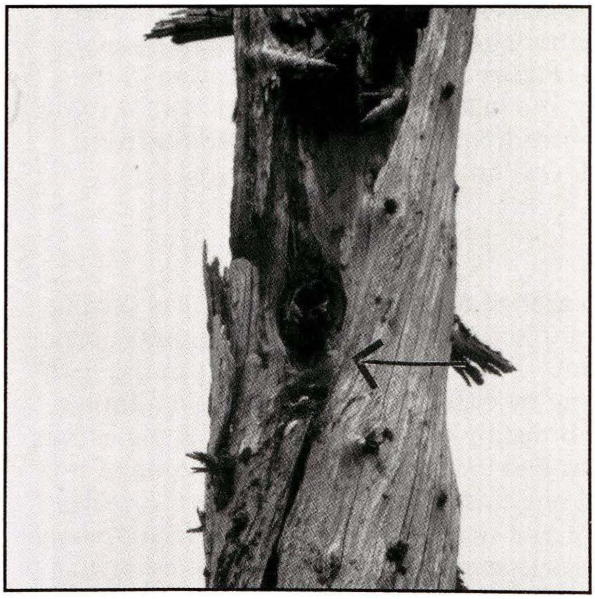

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Figure 3.—*Nest and chicks of Northern Hawk Owl (*Surnia ulula*) in Nova Scotia, Canada. The chicks appear as a mass of gray down at the arrow (June 1996).*

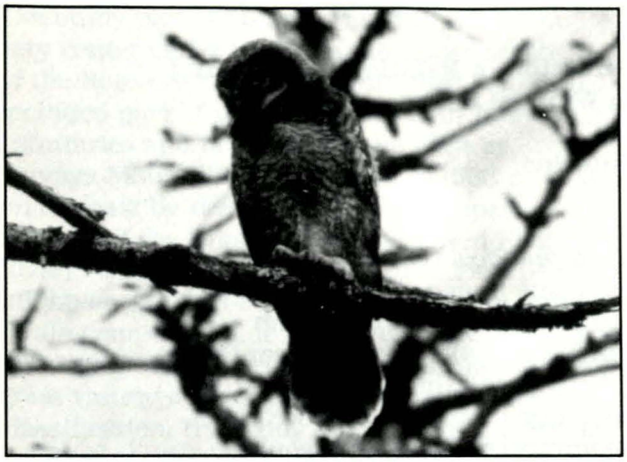
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Figure 4.—*Fledgling Northern Hawk Owl* (Surnia ulula) *in July, 1996, in Nova Scotia, Canada.*

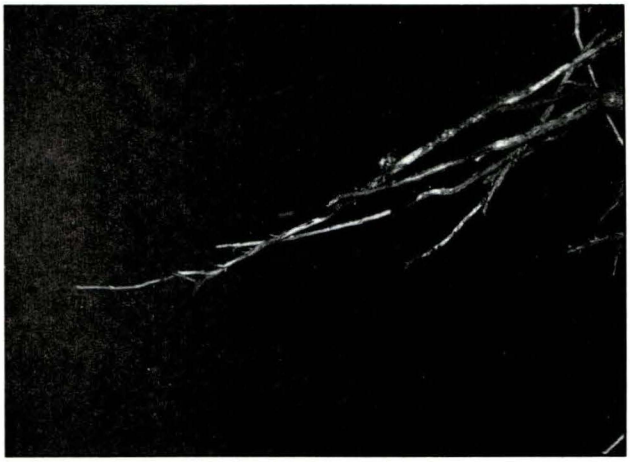
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Figure 5.—*Boreal Owl* (Aegolius funereus) *- first summer record for Nova Scotia, Canada. This is likely a breeding bird.*

It is thought that hawk owls are a recent addition to the avifauna of the province. These birds have likely exploited newly created habitat (spruce budworm defoliated forest) only recently. This assumption is based on the fact that hawk owls are not particularly difficult to find, being large, vociferous, diurnal and prone to perching at the tops of tall trees. Had they bred here before, it is unlikely that they would have been missed.

The Boreal Owl occurrence is the first summer record of this bird for Nova Scotia—it is a bird that authorities "know" nests here, it just has not been documented. We managed to call it in on both the June and July legs of the expedition; on each occasion it responded aggressively. In addition, we found a possible nest cavity in the area. The cavity contained a contour feather of a Boreal Owl. It is felt that a more rigorous search during its breeding season will turn up an active nest.

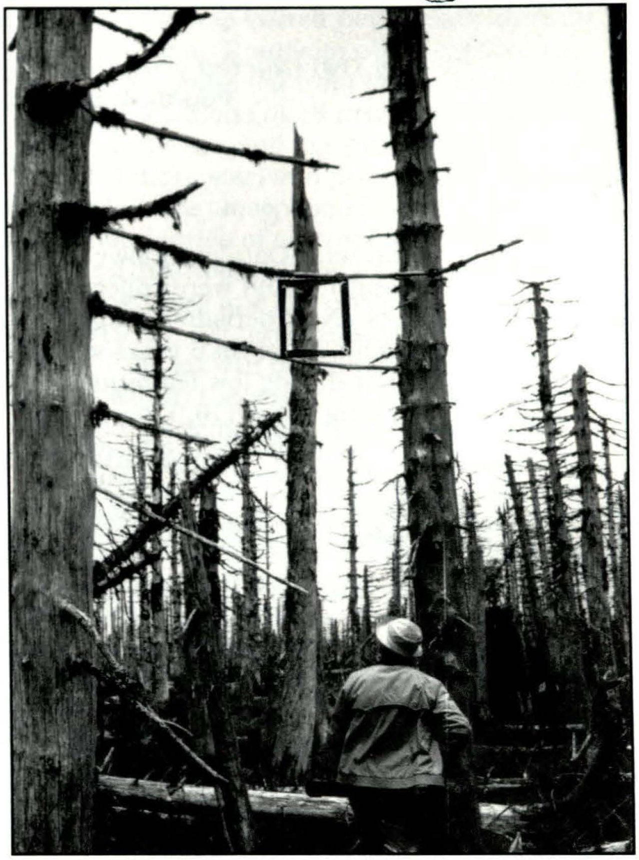
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Figure 6.—*Nesting habitat and nest tree of the first breeding record of the Northern Hawk Owl* (Surnia ulula) *in Nova Scotia, Canada. The outlined area is enlarged in figure 3.*

ACKNOWLEDGMENTS

Thanks go to my colleagues on the expedition, Calvin Brennan, Tony Miller, Vanessa Partridge, Anne Powell and Peter Batt. This work was funded by a Nova Scotia Museum Research Grant.

LITERATURE CITED

Godfrey, W. Earl. 1986. The birds of Canada. Ottawa, ON: National Museum of Canada. 595 p.

Tufts, Robie. 1986. Birds of Nova Scotia, 3d ed. Halifax, NS: Nimbus. 478 p.

Snowy Owl (*Nyctea scandiaca*) Reproduction in Relation to Lemming Population Cycles on Wrangel Island

Irina E. Menyushina[1]

Abstract.—Data on Snowy Owl (*Nyctea scandiaca*) reproduction on Wrangel Island were collected for six seasons from a total of 423 nests. Nest densities ranged from 0.15 to 0.40 nests/km^2. Mean clutch size for all 6 years was 6.5 (from 5.3 to 8.4) being significantly higher during low lemming season (7.17) ($N = 29$) than for peak lemming season (6.0, $p < 0.001$). Clutch size correlated with weather conditions, females' age, and lemming numbers. Number of young fledged per nest was the highest during peak lemming numbers. Bigamous units occurred only during medium, high, and peak lemming numbers. Nestling mortality was due to lack of food.

Snowy Owl (*Nyctea scandiaca*) biology has been studied in different parts of its circumpolar range, including Wrangel Island (Litvin and Baranyuk 1989, Robinson and Becker 1986, Taylor 1974). However, few long-term studies on this species have been conducted (Pitelka *et al.* 1955a,b), and even those did not investigate the whole variety of Snowy Owl population parameters. Watson (1957) suggested that Snowy Owl nest density, clutch size, and reproductive success may differ in different areas even under high lemming population numbers. In most of the previously published articles on Snowy Owl biology, the relationship between the number of nests and clutch size, and lemming numbers is mentioned but without describing the mechanisms of this correlation (Cramp 1985, Johnsgard 1988, Krechmar and Dorogoi 1981, Litvin and Baranyuk 1989, Parmelle 1992, Robinson and Becker 1986, Voous 1988).

This paper presents data on Snowy Owl reproduction on Wrangel Island collected from a permanent study plot (45 km^2) and on routes (3,000 km) for six seasons, 1990-1995, during which lemming numbers ranged from depression to peak.

Objectives of the study were:

1. To determine factors responsible for the density of Snowy Owl reproductive settlements.
2. To investigate relationships between variations in Snowy Owl clutch size and survival of young, and various environmental parameters, including lemming numbers.
3. To estimate the reproductive contribution of females of different age.
4. To investigate occurrence of polygyny in Snowy Owls during different phases of population cycle, and reproductive success in family units of bigamous males.

STUDY AREA

Wrangel Island is situated in the Chukchi Sea 140 km north of Chukotka peninsula between 70° -71°N and 179°W - 177°E. It is the only large land mass in the eastern sector of the Asian Arctic. The island is 7,670 km^2 in size, 4,700 km^2 of which are mountain masses with the highest top of 1,095 m above sea level, surrounded from north and south by open tundra. The climate is rather continental (Svatkov 1970), with average annual temperature below zero (Celsius) and a warm period not longer than 2 months. All types of major arctic landscapes are represented here (Petrovskyi 1967). Two lemming species—the hooted lemming (*Dicrostonix vinogradovi*) and common lemming (*Lemmus sibiricus*)—are the main Snowy Owl prey on the island (Dorogoi 1987).

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The study plot of 45 km^2 was situated in the very center of the island in the upper reaches of the Neizvestnaya River (Unknown River). It included part of the river valley with numerous tributaries and bordered on the west by Pervaya Mountain (first mountain, 503 m) and on the east by the watershed and upper reaches of the Krasnyi Flag River (Red Flag River). Such features as rugged landscape with hilltops up to 200-350 m, differences in substrate composition, in timing of snow melt, and in wetting of the territory cause formation of a great variety of ecotopes. In terms of floristic classification, the study plot reflects the special sub-zonal type with mixed characteristics of typical northern tundras and arctic tundras (Yurtcev *et al.* 1989).

METHODS AND MATERIALS

Observations were carried out in the spring-summer seasons (from May to September) of 1990-1995, during a total of 22.5 months. The length of each observation period varied from 3 to 5 months depending on environmental conditions of the year. Characteristics of the spring conditions and lemming populations are given in table 1. Lemming numbers were estimated by the number of lemming under-snow nests, freshly cleaned den entries and number of lemming carcasses at Snowy Owl nests. Lemming nest and den survey routes crossed all types of habitats and slope exposures, and had a counting strip width of 10 m.

I observed Snowy Owls from blinds positioned within nesting territories, on routes conducted by snowmobiles in various parts of the island during snow-cover periods, or by foot and ATV during snow-free times. Within the study plot all Snowy Owls and their nests were counted, and each nest was visited periodically during the field season. Routes in other parts of the island were conducted from one to three times each. The locations of all nests were mapped. I recorded the sex and age class of birds, based on distribution, size, and density of dark dots on the plumage (Josephson 1980). I determined boundaries of owl reproductive territories by farthest points of male landings (not only on perches) and by territorial displays (Taylor 1973). All territories were mapped. I observed the growth of owl nestlings in all families within the study area; nestlings were provided with temporary individual colored marks and regularly weighed. In 1992-1994, I marked 25 nestlings from 11 different broods with colored patagial-tags. Reproductive success was estimated by the number of nestlings observed to fledge. Total time of observations was 3,700 hours, total length of routes was 3,000 km. During six seasons I examined a total of 423 nests, including 79 in the study plot and its nearest vicinity. The history of 75 nests was known from the beginning to the end of the breeding season.

RESULTS

Timing of Egg Laying

Snowy Owls do not stay on Wrangel Island over winter. Only single birds were rarely recorded on the island during winter in years of very high lemming numbers (Ovsyanikov and Menyushina 1986). The arrival of large numbers of owls to the island begins by mid-May and lasts from 1 to 3 weeks. Weather conditions, timing of snow melt and floods, to which the beginning of the owls' breeding season is related, vary considerably (table 1). Nevertheless, whatever the weather conditions are, the

Table 1.—*Characteristics of spring conditions and lemming populations on Wrangel Island.*

Year	Spring	Beginning of flood[1]	End of snow melting	Lemming number	Phase of lemming population
		dd.mm	*dd.mm*		
1989	?	?	?	?	Depression
1990	Very early	15.05	28.05	Low	Beginning of growth .
1991	Normal	25.05	10.06	Low	*L.s.* decrease, *D.v.* growth[2]
1992	Normal	22.05	10.06	Low	Growth
1993	Normal	22.05	10.06	Medium	Growth
1994	Late	07.06	20.06	High	Peak
1995	Very late	12.06	25.06	Med-High	Decrease
1996	?	?	?	?	Depression

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[1] Dates of flood beginning on Neizvestnaya river.

2 *L.s. = Lemmus sibiricus, D.v. = Dicrostonix vinogradovi.*

majority of Snowy Owls (80.5 percent, n = 142) begin egg laying and incubation within a short period from 15 to 31 May. In late springs, the period when first egg laying and incubation begins is 2-3 times longer than under normal spring conditions—27-30 days against 7-11 days respectively.

Lemming Population Estimation

The number of lemming under-snow winter nests and freshly cleaned den entries positively correlated with each other (r = 0.8861, P = 0.0187). Therefore, these parameters are considered relative indicators of the intensity of lemming under-snow reproduction that determines rodent abundance in the subsequent summer (table 2). For the hoofed lemming, numbers of lemming under-snow nests and cleaned den entries positively correlated with hoofed lemming carcasses at owl nests (r = 0.9188, P = 0.0096 and r = 0.9910, P = 0.0001, respectively). For the common lemming, only the number of under-snow nests positively correlated with the number of common lemming carcasses at owl nests (r = 0.7965, p = 0.0544), whereas den number did not correlate (r = 0.5053, p = 0.3065).

Snowy Owl Nest Density

Snowy Owl population on Wrangel Island fluctuates between years, and has a dynamic spatial and demographic structure (Litvin and Baranyuk 1989, Menyushina and Ovsyanikov 1991). Owl numbers recorded during route surveys across the island ranged from 0.11 to 0.7 birds per km. In the beginning of a breeding season adult birds ready for reproduction arrive first (April-May). Immature owls and adult non-breeders arrive later (June-July). Owl numbers within the study plot positively correlated with owl numbers recorded during route surveys in other parts of the island (r = +0.8363, P = 0.038, fig. 1). However, owl nest densities within the study plot did not positively correlate with the number of owls observed on routes in other parts of the island (r = 0.3663, P = 0.4803). This can be explained by the fact that the spatial distribution of owls in different areas of the island is not equal, being determined by landscape features and food availability (Menyushina and Ovsyanikov 1991). In other words, even when owl numbers are low, the majority of breeding birds are concentrated within the most favorable nesting habitats, whereas spatial patterns of non-breeders are more opportunistic.

Owls nested every year except years of lemming population depression (1989, 1996). Study plot nest densities ranged from 0.15 to 0.4 nests per km^2 (table 3). Nest densities did not positively correlate with the numbers of lemming under-snow nests per hectare (combined data for both species, r = 0.5166, P = 0.2940), nor with the numbers of cleaned dens per hectare (r = 0.1941, P = 0.7125). However, the density of successful nests was positively correlated with lemming numbers (r = 0.8939, P = 0.016). Increased nest density within the study plot was observed during years when the proportion of older females in the breeding population was lower (r = -0.8504, P = 0.0319), and during late spring seasons (r = 0.8020, P = 0.0549). Usually, younger owls and later arriving birds, while choosing a nesting spot, orient themselves on already settled owls. This is evident from the spatial structure of the settlement of breeding owls and from the dates

Table 2.—*Data on lemming nests, dens and carcasses at Snowy Owl (*Nyctea scandiaca*) nest sites on Wrangel Island.*

Year	LWN	N of ha	LCD	N of ha	LC at owl nests	Number of visits to owl nests
	per ha		*per ha*		*D.v./L.s*	
1990	5.1	14	2.1	14	17/15	51
1991	6.4	17	—	—	32/4	49
1992	5.2	17	2.0	17	28/5	64
1993	9.3	17	11.0	11	35/8	75
1994	20.2	15.5	69.0	12	159/31	145
1995	15.4	14	14.6	14	58/46	136

LWN = number of lemming under-snow nests, LCD = number of cleaned dens, LC = lemming carcasses, *D.v.* = *Dicrostonix vinogradovi*, *L.s.* = *Lemmus sibiricus*, N of ha = area (ha) surveyed..

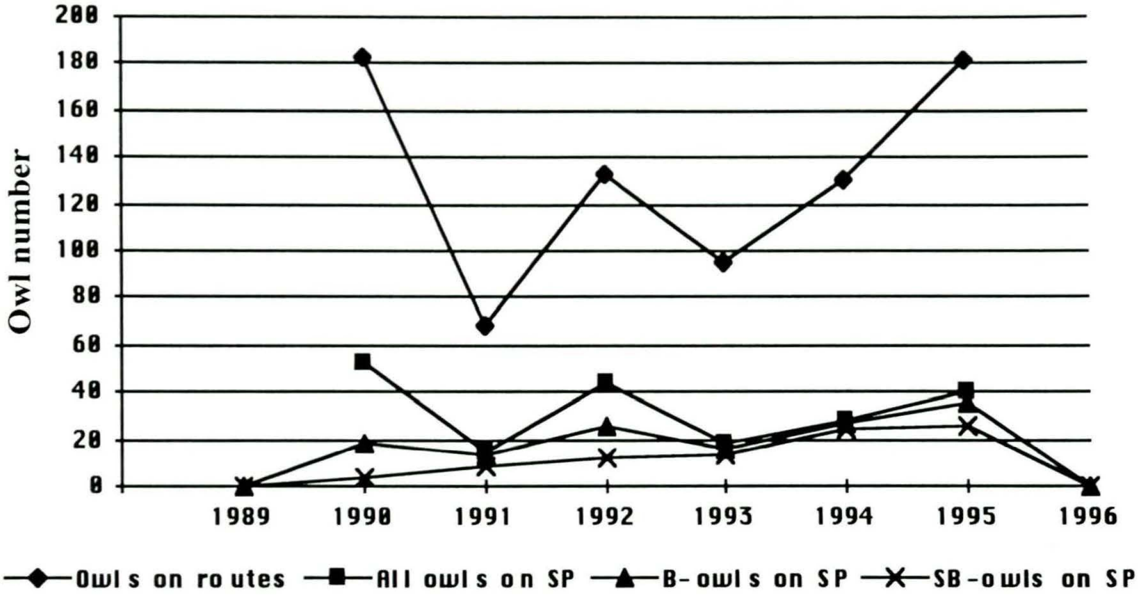

Figure 1.—*Dynamics of Snowy Owl (*Nyctea scandiaca*) numbers on survey routes and in the study plot (SP-study plot, B-breeding, SB- successfully breeding) on Wrangel Island.*

Table 3.—*Snowy Owl (*Nyctea scandiaca*) nest density, mean distance between nests, and mean nesting territory size on Wrangel Island.*

Year	Lemming trend	Lemming number	Owl nest density	Mean nest distance	Range	Territory size	Range
			Number\km^2	*km*		*km^2*	
1989	Depression		?	0	?	?	?
1990	Growth	Low	0.2	1.84	1.2-3.0	2.4	1.3-4.0
1991	Growth	Low	0.15	2.8	1.1-5.2	3.6	2.6-4.5
1992	Growth	Low	0.28	1.5	1.1-2.0	1.9	1.1-2.5
1993	Growth	Medium	0.2	2.17	1.2-3.2	2.3	2.0-2.6
1994	Peak	High	0.26	1.21	0.35-2.2	1.46	0.7-2.5
1995	Decrease	Med-High	0.4	1.46	0.3-2.4	2.48	1.5-6.7
1996	Depression		?	?	?	?	?

of egg laying. Later arriving birds prefer to settle for nesting close to already incubating owls (within 1-2 km), thus increasing the nest density.

The process of breeding settlement formation is, to a great extent, directed by the intensity of the "signal field" [Definition of the term "signal field" is used here in accordance to the concept of N.P. Naumov (1973)] within the owl breeding habitats—by number and distribution of permanent perches and old nest sites. For instance, 81 percent (61 of 75) of all study plot nests were situated in old nest sites.

The density of 0.4 nests per km^2 was a maximum possible nesting density for Wrangel Island, at least for area samples up to 40-50 km^2. Under such high density many territorial conflicts between breeding owls occurred. As a result, one nest had been abandoned by the beginning of the incubation period. Nest densities for smaller area samples (10 km^2) can be even higher—up to 0.7 nests per km^2. Under such conditions one male was killed during the settling period, perhaps in territorial combat.

Clutch Size

Mean clutch size for all research years was 6.5 ± 0.1SE (n = 292). Study plot mean clutch size for all 6 years did not differ from that in other parts of the island (table 4). Therefore, data collected from the study plot is representative for the entire population. Mean clutch sizes for each season in the study plot ranged from 5.8 ± 0.47 SE (n = 18) to 8.4 ± 0.52 SE (n = 7) and were not positively correlated with lemming numbers (r = -0.5990, P = 0.2089) or with owl nest densities (r = -0.6273, P = 0.1824). Mean clutch size during low lemming seasons (7.21 ± 0.15 SE, n = 67) was significantly higher than for peak lemming season (6.0 ± 0.17 SE, n = 48, P = 0.001). Mean clutch size was influenced by a number of factors, in addition to lemmings, such as weather, time of egg laying, females' age, and previous winter conditions.

Mean clutch size in early spring seasons was significantly higher than in late spring seasons (M1 = 8.03, N = 36, M2 = 5.59, N = 39, P = 0.0001). In this calculation, in addition to my own data, I included data collected by the staff of the nature reserve prior to my research.

In all seasons, mean size of clutches with first eggs laid during the period from 15 to 20 May was significantly higher than for clutches with first eggs laid in the period from 26 May to 05 June (M1 = 7.19, N = 16, M2 = 5.89, N = 26, P = 0.003).

For young females, mean clutch size was larger than for middle-age (M1 = 5.52, N = 25, M2 = 6.34, N = 41, P = 0.001) and old females (M1 = 5.52, N = 25, M2 = 6.91, N = 52, P = 0.028) (Josephson 1980).

Although data on Snowy Owl wintering ecology in this region is lacking, wintering conditions appear to influence Snowy Owl clutch size. For example, the winter of 1992-1993 in Chukotka was extremely severe with frequent long blizzards. During the following summer of 1993, when other season characteristics were favorable for normal clutch size, I recorded the lowest clutch size for the entire 6 year period (table 4). Moreover, in the summer, breeding males were unusually passive during both settling and nesting periods. Only 44 percent of all males in that season demonstrated active nest defense and not one of them risked attacking a human intruder.

Male activity also influenced clutch size, perhaps due to successful competition for better nesting territories. During 3 years with low lemming numbers, mean clutch size for nesting males was higher than for non-nesting males (M1 = 7.79, N = 14, M2 = 6.64, N = 14, P = 0.026).

Polygamy

I observed five cases (6.5 percent of all family units observed) of polygamy in the study plot, only during medium, medium-high, and peak lemming numbers. Bigamous families were formed in the absence of male partners on suitable nesting territories (N = 3) and as a result of territorial conflicts (N = 2) in one of which the second male was killed. Hatching in nests of one bigamous family occurred within only 1 day of each other. In all other cases second females started egg laying 10-14 days later than first females. Mean distance between first and second nests in bigamous units

Table 4.—*Variations of* Snowy Owl (Nyctea scandiaca) *clutch and brood sizes in study plot on Wrangal Island.*

Year	WI mean clutch size (±SE)	N	SP mean clutch size (±SE)	N	Range	Mean brood size (±SE)	N	Range
1990	6.37	10	6.78±0.4	9	5-9	0.33±0.23	9	0-2
1991	8.33	21	8.43±0.29	7	8-10	1.71±0.52	7	0-3
1992	6.45	18	6.71±0.3	13	4-9	1.78±0.49	9	0-3
1993	5.79	55	5.78±0.4	9	5-8	2.57±0.72	7	0-5
1994	6.01	32	6.19±0.33	14	3-8	5.50±0.29	14	4-7
1995	5.50	13	5.80±0.25	18	4-8	3.62±0.47	13	0-6

WI- Wrangel Island, SP - study plot.

was 0.85 km (SE = 0.13, range 0.35-1.1 km, N = 5). In all cases, males quit feeding and defending one of the nests or broods before the young fledged. In three cases, the male remained with the first female, in two the male remained with the second. Both nests in bigamous units fledged young only during the peak lemming year. From 10 nests in bigamous families 2 (20 percent) were abandoned by males during incubation. In monogamous families only 9 percent of nests (3 from 35) were abandoned.

Mean clutch and brood sizes in bigamous units did not differ significantly for first and second females (M1 = 5.0 ± 0.01SE, M2 = 5.80 ± 0.37SE, N = 5, P = 0.066 for clutch sizes and M1 = 3.75 ± 0.57SE, M2 = 3.00 ± 0.89SE, N = 4, P = 0.524, for brood sizes respectively).

Mean clutch size in bigamous and monogamous families did not differ significantly (M1 = 5.40 ± 0.78SE, N = 10, M2 = 6.07 ± 0.81SE, N = 35, P = 0.092). However, general reproductive success in bigamous units was lower than in monogamous pairs. Mean fledgling brood size in bigamous units was lower than in monogamous families (M1 = 3.375 ± 0.63SE, N = 8, M2 = 4.687 ± 0.51SE, N = 32, P = 0.038).

Number of fledglings in bigamous units ranged from 3 to 9 (M = 5.40 ± 1.29SE, N = 5). Average number of fledglings per adult male in bigamous and monogamous families did not differ significantly (M1 = 5.40 ± 1.29SE, N = 5 and M2 = 4.69 ± 0.51SE, N = 32, t = 1.115, P = 0.273).

Reproductive Success

Reproductive success was defined as the percentage of fledglings from all hatched nestlings of the brood. From 1990-1995, reproductive success varied from 5 to 96 percent (table 5). Lemming abundance was the major factor affecting owl reproductive success. Successful nest density and mean brood size was positively correlated with lemming numbers (r = 0.8213, P = 0.045 and r = 0.9581, P = 0.0026, respectively). Mean brood size ranged from 0.33 (SE = 0.23) to 5.50 (SE = 0.29) on different phases of the population cycle (table 4). Mean brood size in 1990—the first year after lemming depression—differed significantly from two following seasons of low lemming populations (P = 0.004). A sharp increase in brood size was recorded in the peak lemming season of 1994, when it differed significantly from seasons of medium, 1993 (P = 0.0001) and medium-high, 1995 (P = 0.001) lemming numbers.

All other factors had an insignificant influence on owl reproductive success. Egg or nestling loss was caused by embryo mortality (2.3 percent of eggs, N = 11), failure of egg fertilization (2.3 percent of eggs, N = 11), egg freezing caused by reindeer or musk-oxen grazing in the vicinity of owl nests (1.6 percent of eggs, N = 8), aggressiveness by Snow Geese (*Chen caerulescens*) (towards Snowy Owls whose nests were surrounded by goose nests (1.1 percent of eggs, N = 5) (see Menyushina and Ovsyanikov 1989), and arctic fox predation (1.5 percent of nestlings, N = 6) (see Menyushina 1995). From 50 to 70 percent of all eliminated nestlings died during the first 10 days after hatching due to lack of food. I did not observe cannibalism in Snowy Owls in the form of weak nestling killing, however, already dead nestlings were utilized by the female for feeding surviving ones. In one case, a female cached the carcass of her dead nestling for 2 days before feeding it to the other young. Cold wet weather also influenced nestling survival; during the lemming peak of 1994, under good feeding conditions, 4 percent of all nestlings (N = 3) were lost due to adverse weather.

Table 5.—*Reproductive success of Snowy Owls* (Nyctea scandiaca) *on the study plot, Wrangel Island.*

Year	Nest N	Aborted nests(%)	Eggs	Lost eggs (%)	Nestling N	Fledgling N (%)
1990	9	39 (30)	61	5 (8)	56	3 (5)
1991	7	0	68	5 (7)	63	11 (17)
1992	13	5 (38)	94	24 (26)	70	17 (24)
1993	9	1 (11)	54	7 (12)	47	18 (38)
1994	12	0	94	11 (11)	83	80 (96)
1995	18	3 (16)	104	14 (13)	90	68 (76)

Reproductive Investment of Females of Different Age Classes

Female age was identified by details of plumage in May-June, before active molting. Three age categories were distinguished—young adults, middle-aged adults, and old females. During seasons of low and medium lemming numbers, 30-40 percent of nesting females ceased incubation. Young adult females successfully reproduced only during medium, medium-high, and peak lemming numbers, whereas old and middle-aged females reproduced during all seasons except the lemming depression. Old females comprised the base of reproductive population during the two first seasons following the lemming depression (fig. 2). In 1992, under low lemming numbers, 67 percent of young females abandoned their nests during incubation. Mean brood size did not differ significantly for females of different age categories (for young—M1 = 3,75 ± 0.51SE, N = 12, for middle age—M2 = 2.72 ± 0.78SE, N = 25, for old—M3 = 3.32 ± 0.49SE, N = 28; for M1-M2 P = 0.087, for M1-M3 P = 0.337, for M2-M3 P = 0.586).

Sex Ratio

Sex of fledglings was identified by the shape and size of dark spots on their wing and tail feathers (Josephson 1980). Females prevailed among older chicks in most broods, due to female fledgling survival being higher under low lemming numbers (fig. 3). The most complete data on sex ratio in fledglings was collected during the peak lemming season, when almost all nestlings survived. During that year, the fledgling sex ratio was 1M:1.56F (N = 71). During seasons with medium lemming numbers, the proportion of males and females in broods was equal. For all six seasons, the sex ratio among fledglings was 1M:1.3F (N = 178). The sex ratio of adult owls was 1.3M:1F (N = 820)—opposite of sex ratio in fledglings. Males prevailed among adults in all seasons. This may indicate a higher mortality of juvenile females during the time of dispersal and their first winter. Female Snowy Owls are heavier than males—weight differences become apparent in young owls at 5-6 weeks of age (males: M = 1301g ± 31.2SE, N = 34; females: M = 1625g ± 38.2SE, N = 37; P = 0.001). This difference may result in young female owls being more vulnerable to food shortages during dispersal.

DISCUSSION AND CONCLUSION

Snowy Owl nest densities on Wrangel Island during my study were similar to data from other parts of its nesting range. On Baffin Island, owls had densities of 0.3 nests per km^2 (for 30 km^2 plot) and 0.47 nests per km^2 (for 12.8 km^2 plot) (Watson 1957). Nest densities in Greenland were 0.28 nests per km^2 (for 50 km^2 plot), and 0.7 nests per km^2 on Bylot Island (Cordier *et al.* 1990). For Bathurst Island, Taylor (1974) reported 0.17 nests per km^2 (for 84.5 km^2 plot). On Wrangel Island I observed relatively high and stable nest densities within the study plot on all phases of the population cycle, except lemming depression. This may be explained by three features of the island. First,

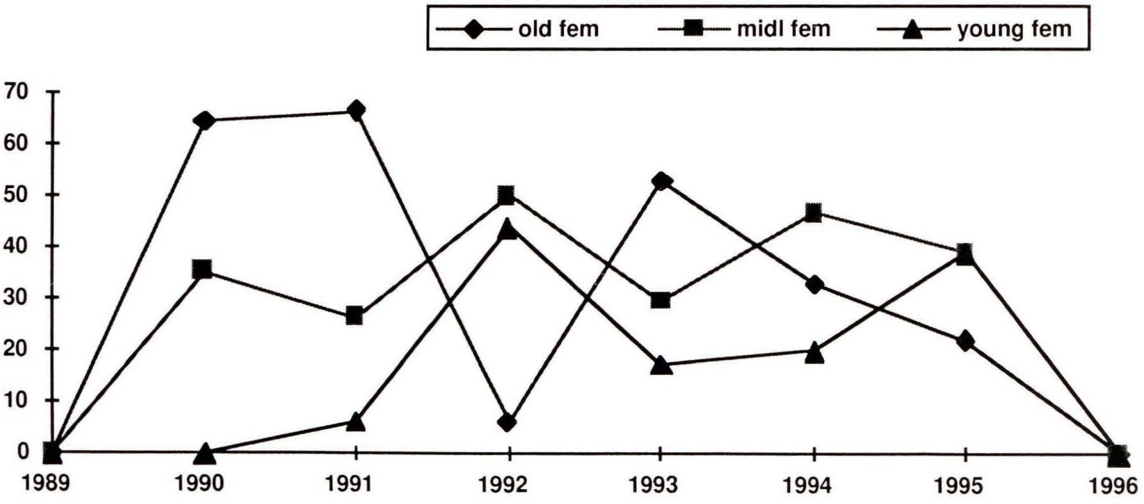

Figure 2.—*Relative number of nesting female Snowy Owls (*Nyctia scandiaca*) of different age (N = 130) on Wrangel Island.*

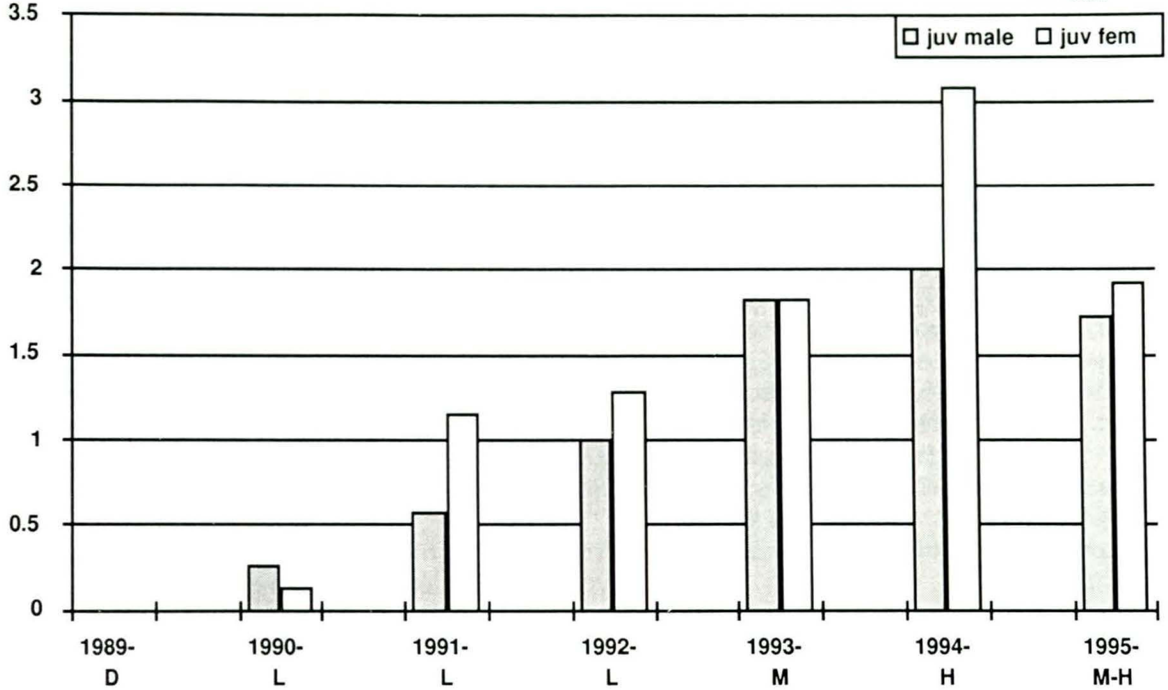

Figure 3.—*Average number of male and female Snowy Owls (*Nyctia scandiaca*) fedglings per brood, on Wrangel Island.*

the island is on the northernmost edge of the owl's nesting area in this region. Therefore, there may be owl accumulation effect—birds arriving in spring cannot disperse farther north-, east-, or westward and have to settle on the island even if lemming numbers are not high enough to maintain the entire breeding population. Second, the island is large enough to represent a variety of suitable breeding habitats. Third, lemming cycles on Wrangel Island are longer than in other areas of the Arctic, with a peak-to-peak period from 5 to 7 years (Chernyavskyi and Tkachev 1982, Krebs 1993). Thus, the whole of Wrangel Island should be considered as a high quality owl breeding area. At the same time, owl nest density at the beginning of the breeding season does not indicate the lemming population number. Only successful nest densities positively correlated with lemming numbers, thereby indicating their population stage.

The lack of correlation between owl nest density and clutch size to lemming numbers, may perhaps, reflect the association of the owls' egg laying activity to lemming surface activity at the onset of the owls' breeding season. On Wrangel Island, most Snowy Owl group

Table 6.—*Time of flood and percent of breeding Snowy Owls (*Nyctia scandiaca*) (N = 127 pairs) on Wrangel Island.*

5 day-periods (dd-dd.mm)	**1990 flood-15.05**	**1991 flood-25.05**	**1992 flood-22.05.**	**1993 flood-22.05.**	**1994 flood-07.06.**	**1995 flood-12.06.**
15-20.05.	55.6	10	7.7	27.8	13.3	24.2
21-25.05	22.2	60	53.8	33.3	20	27.2
26-31.05	11.1	20	38.5	27.8	0[1]	24.2
01-05.06	11.1	10	0	5.6	40	18.2
06-10.06	0	0	0	0	13.3	3
11-15.06	0	0	0	0	13.3	0
16-20.06	0	0	0	5.6	0	3

[1] Snow storm.

copulation is related to the beginning of snow melt (table 6). At that time, most of the land is still covered by snow. Direct observations indicated that owl activity was determined by lemming availability, rather than by absolute number of lemmings within the nesting territory. High levels of lemming surface activity at the onset of breeding is caused not only by high absolute number of rodents, but by snow melting patterns which determines the proportion of snow-free ground and intensity of flood. Starting reproduction under (temporarily) favorable feeding conditions later in summer, Snowy Owls would not have enough prey to raise broods. Due to this factor, owls ready for nesting first settle on slopes with large snow-free areas. Usually, these are slopes of southern exposure with no or little snow accumulation during winter.

Usually, not all of the factors that determine owl clutch size—lemming availability in spring, weather, time of egg laying, female age, and previous winter conditions—are favorable within the same season. Such a situation never happened during my study. However, such a situation occurred in 1981. This coincidence resulted in an outbreak of owl breeding with outstandingly high clutch size (M = 9.71 ± 0.45 SE), which was significantly larger than in all other seasons including other lemming peak years (P = 0.001 compared to peak lemming seasons).

Polygamy in Snowy Owls was reported for Baffin Island (Watson 1957), Hardangervidda, Norway (Cramp 1985) and the Shetland Islands (Robinson and Becker 1986). On Wrangel Island I observed polygamy in Snowy Owls not only during peak lemming numbers, but also during seasons of high and medium lemming populations. My results, however, indicate that polygamy in Snowy Owls cannot be considered a reproductive advantage for the species. For females, occurrence of bigamous units resulted in a decrease in reproductive success. For males, formation of bigamous units may be considered a reproductive strategy aimed to maximize reproductive potential under peak lemming years.

The Snowy Owl's breeding strategy may be characterized as a program to lay the maximum amount of eggs at any opportunity. Laying of as many eggs as possible, in combination with very fast nestling growth (Watson 1957), is considered a species adaptation for badly predictable feeding conditions and a very restricted time frame for reproduction. Final reproductive success, however, depends on summer lemming numbers and is fully realized only during peak lemming years.

The major factor affecting nestling mortality is food limitation. My observations revealed that arctic fox predation has no serious impact on Snowy Owl reproduction on Wrangel Island at any season. This finding refutes an opposing statement of K. Litvin (Litvin and Ovsyanikov 1990) which was made based on irregular examinations of a few owl nests until mid-July only.

The fact that old females can reproduce in all years except lemming depressions may be explained by their better spring condition which results from their hunting and surviving experience (Parmelee 1992). It was shown that the percent of successful hunting in winter was higher for old females than for juveniles (Boxall 1979). Sharp increases of reproductive investment in the owl population during peak lemming years is due to involvement of young females successfully reproducing, whereas reproduction of old females supports the population continuously.

The sex ratio among adult owls and fledglings was reversed. I suggest that the prevalence of females among fledglings may be an adaptation to neutralize higher juvenile female mortality during their first winter to maintain a sex ratio in adult owls closer to 1:1.

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LITERATURE CITED

Boxall, Peter C. 1979. Aspects of the behavioral ecology of wintering Snowy Owls (*Nyctea scandiaca*). Calgary, Alberta: The University of Calgary. 231 p. M.S. thesis.

Chernyavskyi, F.B.; Tkachev, A.V. 1982. Lemmings populations cycles in the Arctic. Ecological and endocrinological aspects. Moscow: Nauka. 162 p.

Cordier, S.; Gilg, O.; Sittler, B.; Spitznagel, A. 1990. Preliminary report of the northeast Greenland expedition "Karupelv valley project" 23 June-3 August 1990. 30 p.

Cramp, S. 1985. The birds of the Western Palearctic. Oxford University Press. 4: 485-496.

Dorogoi, I.V. 1987. Ecology of small mammal predators in Wrangel Island and their role in the dynamics of lemming numbers. Vladivostok: DVO AN SSSR. 92 p. (In Russian)

Johnsgard, P.A. 1988. North American owls. Washington, DC: Smithsonian Institute Press.

Josephson, B. 1980. Aging and sexing Snowy Owls. Journal of Field Ornithology. 51: 149-160.

Krebs, J.C. 1993. Are lemmings large Microtus or small reindeer? A review of lemming cycles after 25 years and recommendations for future work. The biology of lemmings. Linnean Soc. Symp. Ser. 15. Academic Press. Harcourt Brace & Company, Publishers. Chapter 13: 247-259.

Krechmar, A.V.; Dorogoi, I.V. 1981. Snowy Owl (*Nyctea scandiaca*). In: Ecology of mammals and birds in Wrangel Island. Vladivostok: DVNZ AN SSSR: 56-81.

Litvin, K.E.; Baranyuk, V.V. 1989. Breeding of the Snowy Owls (*Nyctea scandiaca*) and lemming numbers in Wrangel Island. In: Birds in communities of the Tundra Zone. Moscow: Nauka: 112-128.

Litvin, K.E.; Ovsyanikov, N.G. 1990. Relation between breeding and numbers of Snowy Owls and arctic foxes, and numbers of lemmings on Wrangel Island. Zoological Journal. 69(3): 1012-1023. (In Russian, English summary)

Menyushina, I.E. 1995. Interspecies relations of the polar fox (*Alopex lagopus L.*) and the Snowy Owl (*Nyctea scandiaca L.*) during the breeding season in the Wrangel Island. III. Lutreola. 5: 15-19.

Menushina, I.E.; Ovsyanikov, N.G. 1989. Negative aspects of waterfowl nesting around Snowy Owl nests. In: Tschernov, Y.I.; Gezen, M.V.; Tishkov, A.A., eds. Interactions of organisms in tundra ecosystems. Summaries of reports; All-Union symposium; 1989 5-8 September; Vorkuta. Sivtivkar: 126-128. (In Russian)

Menyushina, I.E.; Ovsyanikov, N.G. 1991. Spatial distribution of Snowy Owls on Wrangel Island. In: Populations and animal assemblages of Wrangel Island. Moscow: 23-41. (In Russian)

Naumov, N.P. 1973. Signal biological fields and their role for animals. Journal of General Biology. 34(6): 808-817. (In Russian, English summary)

Ovsyanikov, N.G.; Menushina, I.E. 1986. Competition for food between snowy owls, *Nyctea scandiaca*, and arctic foxes, *Alopex lagopus*. Zoological Journal. 65(6): 901-910. (In Russian, English summary)

Parmelee, D.F. 1992. Snowy Owl, *Nyctea scandiaca*. In: Poole, A.; Gill, F., eds. The Birds of North America No. 10. Philadelphia, PA: The Academy of Natural Sciences, and Washington, DC: The American Ornithological Union. 20 p.

Petrovskyi, V.V. 1967. Description of plant assemblages of the central part of Wrangel Island. Botanical Journal. 52(3): 332-343. (In Russian, English summary)

Pitelka, F.A.; Tomich, P.Q.; Treichel, G.W. 1955a. Ecological relations of jaegers and owls as lemming predators near Barrow, Alaska. Ecological Monograph. 25: 85-117.

Pitelka, F.A.; Tomich, P.O.; Treichel, G.W. 1955b. Breeding behavior of jaegers and owls near Barrow, Alaska. Condor. 57: 3-18.

Robinson, M.; Becker, C.D. 1986. Snowy Owls on Fetlar. British Birds. 79: 228-242.

Svatkov, N.M. 1970. Wrangel Island. Soviet Arctic: 459-463, 466-469.

Taylor, P.S. 1973. Breeding behavior of the Snowy Owl. Living Bird. 12: 137-154.

Taylor, P.S. 1974. Summer population and food ecology of jaegers and Snowy Owls on Bathurst Island N.W.T. emphasizing the long-tailed jaeger. University of Alberta. 167 p. M.S. thesis.

Voous, Karen H. 1988. Owls of the Northern Hemispere. Cambridge, MA: MIT Press.

Watson, A. 1957. The behavior, breeding, and food-ecology of the Snowy Owl, *Nyctea scandiaca*. Ibis. 99: 419-462.

Yurtzev, B.A.; Polozova, T.G.; Sekretareva, N.A. 1989. Additions and corrections to the list of higher plants of Wrangel Island. Report 1. Bulletin MOIP. Sec. Biol. 94 (3): 79-89. (In Russian, English summary)

World Distribution of Owlaholics

Heimo Mikkola[1]

Owlaholics are people who collect anything with an owl on it. This paper gives the most common reasons how and why people become addicted to owls and shows their known distribution. Although thousands of owl collectors and enthusiasts reside all over the world, the majority live in Europe and the United States. While no evidence exists of owl collecting clubs in Latin and South America or Africa and Asia, loads of owlaholics live in Australia. Even such far-flung places as Japan and Fiji can claim a few. Since owlaholics are social, active people, this addiction will probably spread even further.

WORLD DISTRIBUTION OF OWLAHOLICS

The International Owl Collectors Club, based in the United Kingdom, has approximately 220 members from 16 countries.

AUSTRALIA	52
BELGIUM	3
CANADA	1
DENMARK	1
FIJI	1
FINLAND	1
GERMANY	7*
HOLLAND	2
JAPAN	1
MALAWI	1
NEW ZEALAND	2
SOUTH AFRICA	1
SPAIN	1
UKRAINE	1
UNITED KINGDOM	34
UNITED STATES	109**
Total	218

* More than 100 owl collectors and enthusiasts are members of the German organization "Arbeitgemeinschaft EULENSCHUTZ".

** In the United States, thousands subscribe to OWLS Magazine, the publication for owl collectors and enthusiasts.

SEXUAL DISTRIBUTION OF OWLAHOLICS

According to Elise Mann, founder of the International Owl Collectors Club, only 20 percent of the members listed above are males, but they seem to own the big collections (5,000 or more items). She concludes that while women are more likely to collect things, men, once hooked, are more likely to become obsessed.

WHY AND HOW PEOPLE BECAME ADDICTED TO OWLS

Below are some common reasons how and why people started collecting every form of owl. Figurines, carvings, statues, and paintings are just a few popular items. Owlaholics admit to sleeping on owl sheets, cooking with owl hot pads, and wearing owl jewelry.

1. Preferring to work the graveyard shift or stay up at night: People whose biological clocks are set "wrong" and are at their mental best between midnight and 06:00 am are called night owls. This connection often gets them interested in collecting owls. For example, a group of nurses used to call themselves the Owl Team and two became collectors.

2. Inheriting an owl collection: Once you have been given a collection, particularly by someone of whom you were fond, not adding to it is hard. This also covers people who started collecting when a family member or a friend passed onto someone duplicates in his or her collection.

3. Being involved with real owls: Like myself and many of you reading this, so we all know how that goes!

4. By accident: Some people suddenly realize they are collecting when they put several owl items together, then start thinking things like, "Humm, I'll buy that. It will go well on my owl shelf or owl wall."

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The Importance of Old Growth Refugia in the Yukon Boreal Forest to Cavity-nesting Owls

D.H. Mossop[1]

Abstract.—The Yukon's boreal forest is a slow-growing yet dynamic system greatly affected by wildfire. Trees of a diameter and age to accommodate cavity-nesting owls and other larger birds should be rare. An experiment was conducted by erecting just over 100 nest boxes throughout the southern Yukon to test the availability of nest holes for small owls. After 5 years an insignificant 1 percent of boxes have been used by Boreal Owls (*Aegolius funereus*). Apparently adequate natural cavities exist. Unique old growth riparian forests are suggested, apparently protected from fire by wetlands. Management and protection of these valuable areas is becoming a priority as pressures are building for human harvest of trees, even in the northern extremes of the boreal forest.

Cavity nesting is clearly a strategy important to the survival of small owls. The Boreal Owl (*Aegolius funereus*) is fairly common throughout the forested areas of the Yukon Territory. Of practical interest is whether cavity availability does, or potentially could, limit their breeding, notably in the northern limits of the boreal forest.

The boreal forest of the Yukon is characterized by relatively low species diversity and discontinuous distribution due to the generally mountainous topography. Generally, black spruce (*Picea mariana*) associations dominate on poorly drained permafrost sites. Trees on these sites rarely reach a size useful to secondary cavity nesting birds. Only on rarer, more mesic sites do white spruce (*P. glauca*), lodgepole pine (*Pinus contorta*), and sometimes balsam poplar (*Populus balsamifera*) and aspen (*P. tremuloides*) attain sufficient size.

The age they must attain in addition to size is another complication. It is generally known that wildfire plays one of the most important roles in the ecology of the boreal forest. Fire history studies suggest about an 80-200 year occurrence rate (Y.S.E.R. 1996). It seems reasonable to assume that in the slow-growing environment of the Yukon, trees living long enough to attain sufficient size (and decadence) to host nesting cavities will be rare. This in turn should cause competitive stress in populations that need them. Potentially exacerbating the problem, in the last decade, a resurgence has occurred in interest by humans to cut both dead trees for firewood and live trees for sawtimber.

A simple test of these ideas was to provide artificial nest cavities. An overwhelming acceptance of the boxes would signal that natural cavities are limiting; a lack of nest box use would suggest the opposite.

METHODS

Over a 5-year period commencing 1984, 105 nest boxes were erected. All had a floor size of 20 cm x 20 cm (8 in.), a cavity depth of 30 cm (1 ft) and a hole size which varied from 8 cm (3 in.) to 10 cm (4 in.). Nest fronts were of natural slabs although a small percentage were rough cut lumber. Boxes were stained brown; overall the plan was to have the boxes blend with the natural forest community.

Boxes were erected in natural forests where trees were of sufficient diameter to hold the boxes, and the canopy suggested suitable owl nesting habitat. Boxes were placed at various heights from the ground averaging 3-4 m. Locations were purposely selected to make revisits easy. In practice, this meant boxes were placed along road and drainage corridors. (An added objective was to provide an accessible breeding population of hole-nesting birds to be used in public interpretation programs.) All boxes were erected in the southern half of the Yukon (south of 66 N. latitude).

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Revisits were attempted annually. Occupancy of boxes visited late in the breeding season were inferred from nest and food debris.

RESULTS

In total, 573 'box-years' have been 'logged' by this work. Virtually all the species expected did make some use of the boxes on occasion:

American Kestrel	*Falco sparverius*
Bufflehead	*Bucephala albeola*
Barrow's Goldeneye	*B. icelandica*
Northern Flicker	*Colaptes auratus*
Red squirrel	*Tamiasciurus hudsonicus*

Significantly, occupancy was much lower than expected (23 percent) and use by Boreal Owls was remarkably low. Barely 1 percent of box-years were occupied by Boreal Owls (table 1). This happened in spite of continuing reports of sightings and specimens retrieved by the public. Singing adults were regularly recorded in the same general locations where unoccupied nest boxes existed.

DISCUSSION AND CONCLUSIONS

Clearly the idea that the population of small owls has been limited by cavity availability has to be rejected. Cavities of sufficient size are probably not as rare in the boreal forest as once thought. The ecological processes responsible for producing these cavities are of interest and undoubtedly critical to maintaining healthy populations of larger secondary cavity nesters.

Old-growth in the Boreal Forest

The notion that unique parts of forest communities may be naturally protected from normal forest-renewing regime (in this case fire), is not a well-studied phenomenon in the boreal forest.

Recently, ongoing wetland research in the Yukon offered an understanding of at least one geological land form which may turn out to be quite widespread. A feature of the recent glacial past of the southern Yukon landscape are large flat-bottomed U-shaped valleys. Many of these now host small relict streams which meander across the flat valley bottoms. Many of the most important wetlands of the mid and southern Yukon are a result of impeded drainage and ice

Table 1.—*Nest boxes available and occupancy by Boreal Owls* (Aegolius funereus), *Southern Yukon 1983-1996.*

	New boxes	Cumulative Box-Years	Occupied	Occupied by Boreal Owls
1983	13	0	0	0
1984		13	6 (6)	1 (1)
1985		26	5 (11)	0
1986		39	4 (15)	2 (3)
1987	23	42	5 (20)	0
1988	4	55	10 (30)	0
1989	3	91	8 (38)	1 (4)
1990	18	131	8 (46)	0
1991	20	170	7 (75)	1 (5)
1992		231	10 (85)	0
1993	4	312	12 (97)	0
1994	10	393	10 (107)	1 (6)
1995		476	14 (121)	0
1996		573	10 (131)	0
(brackets show cumulative values):			23%	1.04%

lens melt in these habitats. Moreover levees are often built by the streams, producing tiny, mesic, very productive forest community sites where some of the largest diameter trees grow.

More recently, it has become apparent that at times these narrow patches of forest in association with riparian wetlands may be true "old-growth". Apparently, wetlands behind such levees may be protecting these forests from wild fire in the more continuous boreal forest. Very old trees with ample cavity development may be a result.

Owls in the Old-growth

It will be important to quantify the importance of these sites as old-growth and to determine the possible link with critical nesting habitat for owls. Most Boreal Owl sightings are made in riparian forests which is not surprising. However, if certain riparian systems are critical for the species' welfare, it will be essential to protect these areas from recent threats.

Old-growth Under Threat

In the Yukon, firewood cutting has been eliminating most dead trees within road corridors near human habitation over the last 10 years. A relatively high proportion of home heating in the Yukon comes from fuel wood; an estimated 20,000 cords are being cut annually for this purpose. Simple economics dictates that forest managers will be moving further afield to meet this demand.

Of more concern is commercial saw log harvest, which recently has seen a surge of interest in the Yukon. About 100,000 m^3 are cut annually and managers dream of a 400,000 m^3 industry (Y.S.E.R. 1996). Most forest ecologists agree this will not be sustainable, and will lead to the elimination of the few riparian forests with suitable nest trees. These valuable patches will be under severe threat unless good preharvest analysis is required and carried out.

Understanding and protecting these unique and critical sites is very likely to be a priority of boreal forest biodiversity management in the immediate future.

LITERATURE CITED

Y.S.E.R. 1996. Yukon state of the environment report, 1995. Yukon Department of Renewable Resources and Environment Canada. 156 p.

Sex and Age Composition of Great Gray Owls (*Strix nebulosa*), Winter 1995/1996

Robert W. Nero and Herbert W.R. Copland[1]

Abstract.—In winter 1995/1996, a nearly continent-wide movement of Great Gray Owls (*Strix nebulosa*) occurred. A sample of 126 owls examined during this period, mainly from northeast of Winnipeg, included a large number from the 1994 hatch-year. If our assumptions regarding molt are correct, 51 birds were from this age class. An inhibited molt condition found in this group suggests a state of inadequate nutrition prior to or during the normal 1995 molt period. We think that a large 1994 hatch and a subsequent food shortage may be factors partly accounting for the 1995/1996 irruption.

The unusually severe winter of 1995/1996 will be remembered by numerous birders and casual observers, both in Canada and the United States, for the numbers of Great Gray Owls (*Strix nebulosa*) that appeared. One enthusiast stated: "...hordes of those ghosts from the Great [sic.] Boreal Forests...invaded southern and central Ontario. There can be no doubt that many hundreds, even thousands, of Great Gray Owls were involved" (Henshaw 1996). Several sources (e.g., Grieef 1996) reported owls in southern Minnesota and Wisconsin, in southern Ontario and Quebec, and a few even in the Maritimes, Iowa, New York, and Massachusetts. The actual numbers of owls involved in this irruption are unknown, but we believe that in Manitoba there were several hundred birds. Duncan (1996) refers to this winter irruption as "one of the largest documented...in central and eastern Canada and the adjacent United States." Korducki (1996) notes for Wisconsin: "While the numbers of Great Grays did not approach the winter of 1987-1988, this year was unique in the magnitude of their wandering."

ONSET OF MANITOBA MOVEMENT

Owls began making an appearance in our area as early as 27 October 1995, when a road-kill was found. In November, seven reports were received; in December, nearly 50. Daily counts included a high of 23 seen on 29 December by one family driving from Powerview to Manigotagan, a stretch of 71 km. On our last outing 13 April, we saw at least 18 on that same road. We went out on 36 days, during which we drove 20,600 km. Our success in finding owls depended on reports from other observers, plus our familiarity with areas likely to be frequented by owls, and our knowledge of their habits. Unlike many previous winters, owls were scarce southeast of Winnipeg. A few birds occurred west of Winnipeg and at least one spent several weeks in Winnipeg, but the largest numbers occurred northeast of Winnipeg within about 135 km.

BANDING OPERATIONS

This was the winter in which we banded more Great Gray Owls than ever before, surpassing our earlier record of 88 owls (winter 1978/1979) (Nero *et al.* 1984) to a surprising 115. All except two, which we banded in northwestern Minnesota, were taken north and northeast of Winnipeg. Also, we have data from one banded by J.R. Duncan, and 10 other owls found dead or injured. Our capture techniques have already been amply described (Nero 1980). In addition to banding and attaching an individual identification tag to each bird, we recorded four measurements and the state of molt of flight feathers (see Duncan 1996). On one exceptional day we banded and processed 13 owls (3 April 1996). The 115 owls we banded were taken as follows: November - 1, December - 8, January - 5, February - 19, March - 45, and April - 42. Inasmuch as we ceased trying after 13 April, when we found 18

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[1] Wildlife Branch, Box 24, 200 Saulteaux Cr., Winnipeg, MB R3J 3W3; and Manitoba Museum of Man & Nature, 190 Rupert Ave., Winnipeg, MB R3B 0N2, respectively.

that we failed to capture, the April success rate—42 owls in 5 days, was high. The lack of success on 13 April may have been due to greater availability of prey; the gradual disappearance of snow on highway rights-of-way increased the vulnerability of small mammals. Of the 126 owls that came to our attention, none was a bird previously banded (though a Northern Hawk Owl (*Surnia ulula*) captured by us at Ft. Alexander on January 6, 1996 had been banded 8 1/2 years earlier in northern Minnesota by Jim and Patsy Duncan). The number of older unbanded Great Grays captured, or found, may mean that these birds originated from outside the Manitoba main study area. Inasmuch as we have several times recaptured birds banded by us in the same winter, we are assuming that birds banded in previous years should be obtainable if present. Our failure to capture any of the many owls banded at nests by the Duncans may simply be due to the larger number of emigrants.

SEX AND AGE

In all, there were 94 females and 32 males. We did not attempt to apply the formula devised by Duncan (1996) to identify the sex of birds, relying instead mainly on measurements. In our experience, males are usually identifiable even before taking their measurements, their smaller feet in the hand being fairly evident. (For dead birds, internal sex organs were checked for verification). The high female sex ratio is not unexpected, given the greater tendency of the females to wander (J.R. Duncan, pers. comm.). We assume that males are as vulnerable to our capture techniques as are females, though nesting males are shy, compared to their mates. Also, there is some possibility that females, needing to build up fat reserves well in advance of the breeding season, may be more actively seeking prey, and hence may be more readily taken.

The basis for aging a Great Gray Owl (apart from a banded one of known age) rests in the distinctive flight feathers (wings and tail) of the juvenile bird (see Duncan 1996). Thus, one can always identify a juvenile, that is, a bird hatched in the previous summer. The nature of molt in this species is such that normally not all of the juvenal feathers are replaced, some being retained for one or two or more successive years. As long as a juvenal feather is present it is possible to estimate that bird's age. The gray tip that distinguishes the juvenal feather, however, is subject to wear, especially on the longer primaries (no's. 4-9). Once that tip is worn away, it may no longer be possible to recognize the juvenal feather. (The no. 10 primary, it should be noted, unlike any of the other flight feathers, lacks the gray tip altogether). Given that adult-type feathers also are not all shed in any one year, older birds will bear feathers that show, by degree of newness, fading and abrasion, three or more age classes, hence presumed years. Usually, older birds can be aged by this means up to 3-4 years. In the absence of a juvenal feather, however, such birds can only be considered old adults, that is, more than 3-4 years of age.

Only four birds in our sample were juveniles, birds hatched in summer 1995. In that year, the Duncans checked 126 nesting platforms, none of which was in use (pers. comm.), thus it is not surprising to find so few birds from that season. Usually, we identify owls as either adults or juveniles, regardless of sex. Some adults, still bearing one or more juvenal feathers, could be considered adults 3-4 years of age, or, in the absence of any juvenal feathers, "old" adults. In winter 1995/1996, however, we soon recognized a third class which we considered to be 2-year-old birds, a group not previously recognized (probably overlooked). Fifty-six of the birds we examined had hatched in summer 1994 (if our assumptions regarding molt are correct). In that season, the Duncans recorded seven active nests out of 103 platforms checked (pers. comm.). These 2-year-old birds (more correctly, 1 1/2 years old) had mainly juvenal flight feathers, and at first glance one might suppose them to be juveniles, that is, less than 1 year old. The presence of adult-type or non-juvenal innermost secondaries, however, pointed to what we presumed to be their correct age. In their first major molt period, in summer 1995, these birds had replaced only a fraction of the number of flight feathers normally renewed. (Note that we are dealing here mainly with flight feathers, the general contour feather molt being more complicated than this suggests). A tame, captive bird ("Lady Grayl") of known age (and on a steady diet) had, by its second winter, replaced 41 out of 58 juvenal flight feathers (12 rectrices, 9 primaries, 20 secondaries). By contrast, many of the 2-year-old birds we captured had replaced only a dozen feathers or even less. Several of these birds had also retained from

one to five presumed juvenal undertail coverts; these were so badly worn that only a bare shaft remained. These feathers, to use Kay McKeever's aptly descriptive term, were "skeletonized" (pers. comm.). These skeletonized feathers supply the additional confirmation of age; it seems unlikely that such severe wear could occur in 3-6 months or less (from completion of molt to winter). No other explanation seems plausible, in our opinion, for the condition of these 2-year-old birds. Eighteen of these supposed 2-year-old birds also had replaced one or both no. 5 primaries; a few had replaced primaries no. 4 and 6.

The variation in numbers of replaced flight feathers may reflect variable nutritional levels and/or energy demands. In a study of the Tawny Owl (*Strix aluco*), Petty (1994) related inhibited molt to nesting activity, that is, with an abundance of prey there was increased nesting activity and those birds shed fewer feathers than usual. However, as pointed out by Jim Duncan (pers. comm.) few Great Gray Owls breed in their second summer. Hence, it is likely that our surmise regarding molt and nutrition in these 2-year-old birds is correct. This is further substantiated by the scarcity of young from summer 1995 in our sample (four). The inhibited molt shown in these 2-year-old birds was presumably the result of a nutrient shortage (lack of sufficient food) in winter 1994/1995, and/or spring and summer 1995. As a result, these birds had retained much plumage that was more than 1 year old, hence largely worn and faded, thus giving them a strongly brown color overall. Often such birds could be identified at a distance, whether perched or in flight. Wherever these birds originated, and they could have come from many hundreds of km northwards, presumably they had faced a severe shortage of prey. The same nutritional stress factors that inhibited molt in the 2-year-old birds, presumably also affected older birds. But inhibited molt in such birds, especially in the absence of any juvenal feathers, would be less apparent.

CONDITION OF BIRDS

Although body weight has only limited value in assessing the condition of birds, there is a suggestion that as winter progressed, many birds in our sample either lost weight or failed to gain adequately. Adult female weights from November 1995 through February 1996, with one exception, ranged from 1,200-1,500 gms. During March and April, however, 34 birds were handled that weighed less than 1,200 gms. Presumably, increased difficulty obtaining prey, owing either to prey declines, increased snow depth or a combination, played a role. Also, it was during this period that a few obviously thin and weak birds were found.

MOVEMENT DATA

A bird that we banded north of Pine Falls on 24 February 1996, was found dead on 22 March more than 150 km to the southeast in the Moose Lake area (ironically, the capture and banding of this bird had been shown earlier on the CBC-TV program "Coleman & Co."). The bird was found on a well-travelled snowmobile trail, and it had presumably been hit by one of those vehicles. An adult female (one of the 2-year-olds), its weight had dropped by 475 gms. If that weight loss occurred before its accidental collision, then it must have been having difficulty finding food. This band recovery indicates that in late February, owls were still moving southwards. Other, later records, suggest a northward movement, as if birds were returning to their place of origin. For example, an old adult female owl (no juvenal flight feathers) banded on Maple Creek Road west of Lac du Bonnet on 28 December 1995, was recaptured in the same place on 5 April 1996; on 9 April, however, we found this bird (identified by its tag) about 50 km to the north.

CONCLUSION

The indication of failing food supply in summer 1995, as suggested by the molt condition of 56 2-year-old birds, is supported by the scarcity of young in our sample (4 out of 126). Thus, we can suggest a vole shortage, through winter 1994/1995 and summer 1995, over much of the region. This, in itself, could have triggered the movement or irruption of owls in winter 1995-1996. According to Jim Duncan (pers. comm.) red-backed vole (*Clethrionomys gapperi*) populations in southeastern Manitoba and adjacent Minnesota were moderately high in 1993, crashed in 1994 and remained low through 1995 and 1996; meadow vole (*Microtus pennsylvanicus*) populations were very low in 1995, then rose sharply in 1996. Thus, the nature of the 1995/1996 Great Gray Owl irruption, and perhaps earlier ones as well, might be ascribed to levels of prey populations and owl productivity, coupled with severe winter conditions, though the weather factor may be the lesser aspect.

ACKNOWLEDGEMENTS

We thank the numerous persons who reported owl sightings and injured or dead birds. Bert Dacquay kindly brought in the banded owl he found dead on a snowmobile trail. For critical review of the manuscript we thank James R. Duncan and Robert E. Jones. We especially thank our respective wives, Beverly Copland and Ruth Nero, for support and for encouraging us to spend so much time, and money, out looking for owls. Betty Struthers typed the final draft.

LITERATURE CITED

Duncan, J.R. 1996. Techniques to sex and age Great Gray Owls. Birders' Journal. 5: 240-246.

Grieef, G. 1996. Bird news. Manitoba Naturalists Society Bulletin. 22: 10.

Henshaw, B. 1996. A winter to remember. Pickering Naturalist. 21: 56-59.

Korducki, M. 1996. Great Gray Owl update. The Badger Birder. (Wisconsin Society of Ornithologists Newsletter) 440: 1.

Nero, R.W. 1980. The Great Gray Owl: phantom of the northern forest. Washington, DC: Smithsonian Institute Press. 167 p.

Nero, R.W.; Copland, H.W.R.; Mezibroski, J. 1984. The Great Gray Owl in Manitoba, 1968-83. Blue Jay. 42: 130-151.

Petty, S.J. 1994. Moult in Tawny Owls *Strix aluco* in relation to food supply and reproductive success. In: Meyburg, B.U.; Chancellor, R.D., eds. Raptor conservation today. WWGBP, The Pica Press: 521-530.

Observations of Wintering Snowy Owls (*Nyctea scandiaca*) at Logan Airport, East Boston, Massachusetts from 1981-1997

Norman Smith[1]

Abstract.—Snowy Owls (*Nyctea scandiaca*) wintering at Logan International Airport were studied over the 15-year period of 1981-1997. Two-hundred twenty-seven Snowy Owls were banded and color-marked to examine the length of time individual birds stayed at this location and to track the movements elsewhere. Fifty-six owls were re-observed outside of the airport vicinity, and 11 of these were observed more than 150 km away. Dietary preferences based on observations of hunting and feeding owls recorded a total of 192 individuals of 35 species or species types. Educational programs are an important part of the ongoing research effort underway at the airport.

Since 1981, countless days and nights, in every imaginable weather condition, have been spent observing, capturing, banding, and color-marking Snowy Owls (*Nyctea scandiaca*) at Logan International Airport (fig. 1). Snowy Owls usually arrive at the study site in early November and depart in late April. Observations of roosting, hunting, and intraspecific interactions were recorded. Owls were captured when possible to obtain data for the study.

Observing wild Snowy Owls documents their habitat needs, dietary consumption, and nomadic existence. To continue observations after sunset, an ITT 3rd generation night vision scope was used. Hunting techniques and chronology, diet, movements, and social interaction with other owls, were primary interests of this project.

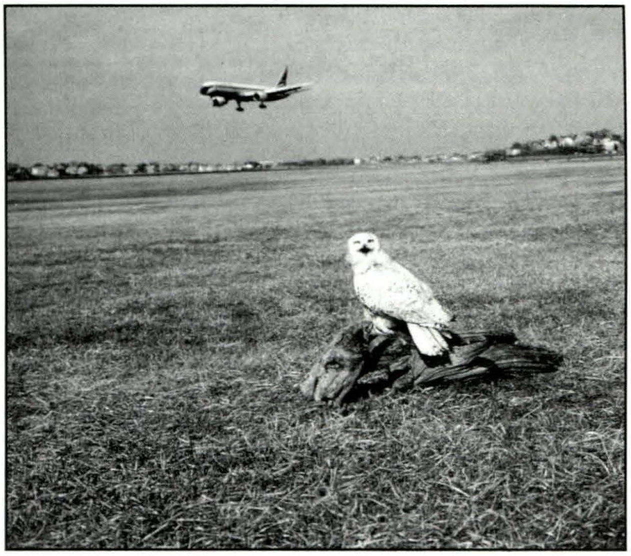

Figure 1.—*Snowy Owl (*Nyctea scandiaca*) at Logan International Airport, Boston, MA.*

Owls have always fascinated me and this was a unique opportunity to learn more about wintering Snowy Owls. I undertook this study to answer the following questions:

- When do the owls arrive at the airport each year?
- How long do they stay?
- How many pass through each winter?
- What do they feed on?
- What are their roosting and hunting habits?
- Do the same birds return to the airport each year?

Trapping can also help determine the distance at which a Snowy Owl can see prey. From observation, we know that Snowy Owls can find rodents under snow without seeing them. We do not know how far away they can hear prey under snow with the noise at Logan Airport. Data collected through trapping these birds provides answers to these questions, and how individual birds adapt to a changing environment.

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[1] Director, Blue Hills Trailside Museum and Chickatawbut Hill Education Center, Massachusetts Audubon Society, 1904 Canton Avenue, Milton, MA 02186.

STUDY AREA

The study was conducted at Logan International Airport in East Boston, MA, latitude 42°22N and longitude 071°01W. The 13th busiest in the world, the airport encompasses approximately 1,053 ha including roadways, terminals, parking garages, runways, and a weather station. The airfield has 729 ha of short, mowed, rolling grassland habitat which supports a large rodent population. On three sides, the open water of Boston Harbor and salt marsh surround the airfield, attracting a number of waterfowl and shore birds. The fourth side is the approach from the city, with the skyscrapers of downtown Boston providing the landscape backdrop. Average precipitation and temperature from November through April are 670 mm and 3°C. A variety of communication and instrument structures provide excellent hunting perches, while rolling grasslands provide good roosting locations.

METHODS

Permission to gain access to the restricted airfield to conduct the study was obtained through the airport's governing body, the Massachusetts Port Authority. This included a background security check, the acquisition of a special driver's license, and a $1,000,000 liability insurance policy.

Equipped with a night vision scope, spotting scope, and binoculars, visual observations of owls were made from a vehicle used as a blind, beginning with the first arrival and continuing until the last bird had departed.

Owls were captured using a manually-triggered 1.5 m diameter spring-loaded bow net placed on the ground. Live bait birds or rodents were placed in a wire cage and the cage situated in the center of the bow net. The trap was triggered from the vehicle after an owl had landed on the bait cage. Each owl captured was banded with a U.S. Fish and Wildlife Service numbered band. The bird was weighed, wing and tail measurements taken, sex and age estimates recorded, and external parasites collected. Each bird was color-marked with a temporary dye on the back of its head, photographed, and released.

The birds were color-marked to allow easy identification of individuals. Color-marking was initially done applied to the birds' chests; however, this method proved unreliable when a bird under observation was facing away from the observer. Color-marking on the back of the head was more successful; when the bird faced the observer it eventually turned its head to survey its surroundings. The color-marking wore off in approximately 6 months leaving only the leg band to identify individuals.

Data gained from trapping and banding birds included the age, sex, and physical condition of Snowy Owls who sojourn at Logan International Airport.

RESULTS

In 15 years, the earliest arrival of a Snowy Owl was October 24 and the latest departure was July 7. These being the exception, the majority of Snowy Owls arrived in mid-November and stayed until late April.

The number of owls observed each winter varied, from lows of five during the winters of 1980-1981 and 1995-1996, to a high of 49 in 1986-1987. On the morning of 23 January 1987, there was a record high of 23 Snowy Owls on the airfield at one time. To date, 227 captured Snowy Owls have contributed data to this ongoing study. Ten owls were re-trapped at Logan from 1 to 10 years after their initial capture.

Color-marking has established proof that these migrant owls travel extensively, with many of the birds being observed in other New England locations throughout the season and identified by their color-mark. A total of 56 sightings of color-marked Snowy Owls have been reported from Maine, New Hampshire, Vermont, Massachusetts, Rhode Island, Connecticut, New York and Delaware. Eleven of these 56 owls were re-observed more than 150 km from the airport (table 1). One particular bird was captured at Logan Airport on 9 November 1991, and color-marked green. It was photographed in Bath, Maine, on 19 December 1991, 197 km northeast. On 24 January 1992, the bird was back at Logan. It was then sighted on Martha's Vineyard, Massachusetts, on 25 February 1992, 115 km southeast of Logan and in

Table 1.—*Reports of color-marked Snowy Owls (*Nyctea scandiaca*) 150 km or more from Logan Airport, Boston, Massachusetts.*

Last date at Logan	Next date/location observed		Number of km/direction from Logan	
01/11/85	02/16/85	Montauk Point, New York	160	SW
12/09/86	01/30/87	New London, Connecticut	155	SW
12/27/86	02/01/87	Fire Island, New York	250	SW
12/28/86	03/07/87	Woodstock, Vermont	185	NW
02/22/87	03/19/87	Watertown, New York	430	NW
11/30/87	01/25/88	Lewes, Delaware	550	SW
02/13/88	03/14/88	Winooski, Vermont	195	NW
01/31/88	03/29/88	Rochester, New York	555	W
07/07/90	07/08/90	Squam Lake, New Hampshire	155	NW
11/09/91	12/19/91	Bath, Maine	197	NE
02/04/93	03/11/93	Sharon, Vermont	195	NW

Charlestown, Rhode Island, on 26 February 1992, 92 km east of Martha's Vineyard. The lighthouse keeper at Boston Light, Little Brewster Island, Massachusetts, photographed the bird on 16 March 1992, 125 km northeast of Charlestown, Rhode Island. The bird was again back at Logan Airport on 23 March 1992, 6 km west of Boston Light and was seen at this site on a regular basis until it departed Logan on 20 May 1992. Other birds; however, have stayed at the study site the entire season.

Seven immature banded Snowy Owls have been recaptured at the study site the following year, one was recaptured at the site 2 years later, and one 6 years later. Most recently, in February 1997, an adult male Snowy Owl was captured and identified as a bird that had been banded at the same site 10 years earlier as a SY[2] bird. In Canada, birds banded at Logan Airport have been recaptured in subsequent years in Ontario and Toronto, and recoveries of dead birds which had been shot have been made in Quebec and Nova Scotia.

Through observation, it has been noted that Snowy Owls prefer to roost on the ground during the day. As the sun sets, they become very active, stretching their legs and wings, and generally will regurgitate a pellet in preparation for their evening hunt. They then locate a perch from which to hunt under the cover of darkness. In addition to hunting from a perch, they will also use a hovering technique similar to a Rough-legged Hawk (*Buteo lagopus*). With the night vision scope, they can be watched throughout the night. Over the course of the study, Snowy Owls were observed capturing or feeding on 192 prey items of 35 species or species types (table 2). They prefer to take their prey on the wing much like a large falcon. Extremely agile, Snowy Owls have been observed outmaneuvering Snow Buntings (*Plectrophenax nivalis*) and overtaking American Black Ducks (*Anas rubripes*) in flight. The largest observed kill was that of a Great Blue Heron (*Ardea herodias*), and the heaviest a Canada Goose (*Branta canadensis*). Other raptors the Snowy Owl has captured are American Kestrel (*Falco sparverius*), Northern Harrier (*Circus cyaneus*), Short-eared Owl (*Asio flammeus*), Barn Owl (*Tyto alba*), and one has even been observed feeding on another Snowy Owl.

Snowy Owls have demonstrated their keen eyesight and hearing during this study. In one instance, a Snowy Owl was observed diving into 20.3 cm of snow and coming up with a vole, which was not visible from the surface. The owl must have heard the vole under the snow. The amazing aspect is that a 747 passenger jet was thundering down the adjacent runway at the same moment. Another Snowy Owl, barely visible to the human eye using 10 x 50 binoculars, somehow managed to spot a European Starling (*Sturnus vulgaris*) in the bow net after dusk had fallen and flew 1.6 km across the harbor for the bait.

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[2] Term SY is used by the Bird Banding Lab to characterize a bird in the second year of its life.

Table 2.—*Prey items which Snowy Owls (*Nyctea scandiaca*) have been observed feeding on or capturing at Logan International airport, 1981-1997.*

Common name	Scientific name	Number of observations
American Black Duck	*Anas rubripes*	23
American Kestrel	*Falco sparverius*	2
American Oystercatcher	*Haematopus palliatus*	1
Barn Owl	*Tyto alba*	1
Black-bellied Plover	*Pluvialis squatarola*	2
Brant	*Branta bernicla*	2
Bufflehead	*Bucephala albeola*	1
Canada Goose	*Branta canadensis*	1
Clapper Rail	*Rallus longirostris*	1
Common Goldeneye	*Bucephala clangula*	1
Double-crested Comorant	*Phalacrocorax auritus*	1
Dunlin	*Calidris alpina*	8
Eastern Meadowlark	*Sturnella magna*	2
European Starling	*Sturnus vulgaris*	5
Great Blue Heron	*Ardea herodias*	1
Herring Gull	*Larus argentatus*	1
Horned Lark	*Eremophila alpestris*	2
Killdeer	*Charadrius vociferus*	6
Muskrat	*Ondatra zibethicus*	7
Northern Harrier	*Circus cyaneus*	2
Norway Rat	*Rattus norvegicus*	47
Red-breasted Merganser	*Mergus serrator*	5
Ring-billed Gull	*Larus delawarensis*	4
Ring-necked Pheasant	*Phasianus colchicus*	2
Rock Dove	*Columba livia*	13
Short-eared Owl	*Asio flammeus*	5
Snow Bunting	*Plectrophenax nivalis*	4
Snowy Owl	*Nyctea scandiaca*	1
Striped Skunk	*Mephitis mephitis*	3
Upland Sandpiper	*Bartramia longicauda*	1
Unidentified species of fish		2
Unidentified species of rabbit		1
Unidentified species of scaup		2
Unidentified species of vole, mice or shrew		31
Unidentified species of yellowleg		1

CONCLUSIONS

The number of wintering Snowy Owls at Logan Airport varied greatly from year to year. In years when many owls were observed and captured, most of them were immature birds and appeared to be in good physical health and body weight. This observation could indicate that there may have been an abundant food supply on the breeding grounds, which in turn resulted in a large number of young hatched and therefore an abundance of Snowy Owls here. The years when few owls were observed, a high percentage tended to be underweight adults, which perhaps means that food had been scarce on the breeding grounds and few young were produced, the result being fewer owls wintering here. Of the 227 owls captured 19 were adult males, 14 adult females, 102 immature males, 81 immature females, and 11 were of undetermined age and sex. More observations need to be done to see how the lack of, or abundance of food on the breeding grounds might affect the numbers of wintering birds. The number of owls observed and captured at Logan Airport has made this the largest known wintering population of Snowy Owls in New England. Even after 15 years spent on this study, it is still hard to imagine that an airport, with all its activity, mega decibel sound levels, and constant jet fumes provides one of the best locations in New England for observation of and research on these magnificent raptors.

Color-marking and banding of Snowy Owls at this location has provided important data about this species. It has also presented more questions which require further exploration about this bird's erratic and nomadic habits, visual range, and hearing capacity. While it is now known that these birds travel extensively during the non-breeding season, and sometimes return to the same wintering site annually or even several years later, it is not known where they go during the more frequent intervals when they are not sighted or captured at Logan and elsewhere.

Examination of 5,039 pellets collected at the study site revealed the most common prey items; Norway rat (*Rattus norvegicus*), meadow vole (*Microtus pennsylvanicus*), and American Black Duck. An examination of these pellets has yet to be summarized. Other prey items include small birds, waterfowl, shorebirds, insects, fish, mice, muskrats, skunks, and even other owls. Observation of Snowy Owls capturing and consuming large prey items has revealed that they tend to eat out the breast cavity, taking in small amounts of roughage which leave minimal traces in pellets. Therefore, visual observation must be included to determine an accurate account of their diet.

EDUCATIONAL PROGRAMS

In addition to gathering data about wintering Snowy Owls, a second objective was to use the information and photographs of the research in a way that would stimulate and educate as many people as possible about the natural history and importance of owls. Yearly bus tours of the airfield in search of Snowy Owls are very popular, especially for the Boston residents who live in the city and have always thought of the airport only as a source of noise and pollution. The tours give them an opportunity to appreciate and understand the habitat and wildlife encompassing the airport. Presentations on this Snowy Owl project using slides, and live birds when available, are done as a regular program at the Blue Hills Trailside Museum[3] for groups of both children and adults. These programs increase the general public's awareness and appreciation for owls and their habitats.

I was fortunate to have two young assistants eager to help me with this study, my daughter, Danielle (fig. 2), now 16, and son, Joshua (fig. 3), now 13. Both are raptor enthusiasts who share my admiration and respect for these creatures and who have been active in my research since they were small children. When small, one of their many tasks was collecting pellets from roost sites. As they grew older, they also assisted in the capture, banding, and color-marking aspects of the study. I now find myself in the role of assistant, as Danielle has started her own project on migrating owls and has captured and banded 96 owls of 7 species. They have both given me a new appreciation for how energetic and resourceful young minds can be. I realize now, more than ever, how important it is to provide education about our

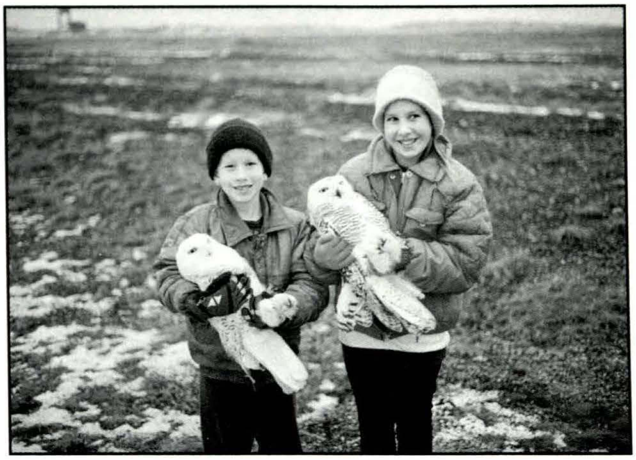

Figure 2.—*My assistants Danielle and Joshua holding Snowy Owls for banding.*

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[3] Blue Hills Trailside Museum is a natural history museum located in the2,756 ha (7,000 acre) Blue Hills Reservation, 3.2 km (2 miles) Southeast of Boston. It is owned by the State of Massachusetts and managed by the Massachusetts Audubon Society.

environment and all that inhabit it; especially to our children so that they can learn to appreciate, protect, and preserve it for us as well as for future generations.

ACKNOWLEDGMENTS

Special thanks to my two "assistants", daughter, Danielle, and son, Joshua, who have made valuable contributions to the research and study of Snowy Owls. Thanks also to my wife, Nancy, who over the past 20 years has encouraged me to pursue my interest in owls. David Johnson did much to improve the quality of this manuscript.

Figure 3.—*My assistant Joshua with an immature (second year) Snowy Owl, left. Joshua with the same Snowy Owl 10 years later, right.*

Using Tape Playback of the Staccato Song to Document Boreal Owl (*Aegolius funereus*) Reproduction

Dale W. Stahlecker[1]

Abstract.—Tape playback of the staccato song of the Boreal Owl (*Aegolius funereus richardsoni*) proved useful in attracting fledglings of both North American *Aegolius* species. No Boreal Owl nests were found in 8 hours of daytime searches. However, six Boreal Owls, including three to four fledglings at two locations, one Northern Saw-whet Owl (*A. acadicus*) fledgling, and an unidentified *Aegolius* responded to tape playback in 16 hours of systematic surveys during the post-fledging period (15 July to 30 August) of 1992 and 1993 in habitat known to be occupied by Boreal Owls. This method is considerably less costly than other means of documenting breeding by this species and may prove useful for other owl species as well.

Boreal Owls (*Aegolius funereus*) were long thought to be denizens of circumpolar northern forests (AOU 1957, Mikkola 1983), but in the past 4 decades have been found in suitable habitat in the mountains of the Pacific Northwest (Whelton 1989) and throughout the Rocky Mountains (Hayward and Hayward 1993). Recently, their southern North American distributional limits in the Rocky Mountains of New Mexico were described (Stahlecker and Duncan 1996).

Although their North American range is now mostly defined, documentation of Boreal Owl breeding activity has proven more difficult to obtain. Boreal Owls are relatively secretive birds, nesting in cavities in forests that include numerous potential nest trees. During an intensive study in central Idaho, 17 of 21 nests in natural cavities were found because the female (14) or male (3) was radio-tagged (Hayward and Garton 1983, Hayward *et al.* 1993). Only four natural nests (2 consecutive years for one site) were found in another intensive study in north-central Colorado (Palmer and Ryder 1984, Ryder *et al.* 1987). Hayward *et al.* (1993) utilized > 300 nest boxes in Idaho to monitor breeding populations in managed forests, and in the process extended the area in Idaho with documented nesting locations. Another large nest box array (> 400) was used to document Boreal Owl nesting in western Colorado (Schulz and Holland, in review). Nest boxes are also extensively used to study Tengmalm's Owl (*A. f. funereus*) in Europe (Mikkola 1983, Korpimaki 1984). Chance encounters with fledgling Boreal Owls in Montana (D. Shea in Rogers 1973), Washington (Batey *et al.* 1980), northern Colorado (Baldwin and Koplin 1966), and southern Colorado (Rawinski *et al.* 1993) have also documented reproduction in those areas. Throughout much of its North American range, however, proof of breeding by the Boreal Owl is lacking, though inferred from the presence of singing males (Hayward *et al.* 1987, Stahlecker and Rawinski 1990).

During Boreal Owl distribution studies in New Mexico, I wanted to locate active nests to prove breeding in the state. In June 1987 and 1992 I attempted to locate active cavity nests of Boreal Owls near trees where males sang spontaneously in April of the same years. Two of us spent approximately 2 hours searching each site, walking slowly through the forest looking for cavities, then knocking softly in imitation of a foraging woodpecker in an effort to elicit a response from a nesting owl. No Boreal Owl nests were found.

On 13 August 1992, while conducting distribution surveys for Boreal Owls with tape playback (Palmer and Rawinski 1986) in the Gila Wilderness Area of southwestern New Mexico, two fledgling Northern Saw-whet Owls (*Aegolius*

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acadicus) followed us for > 800 m and 45 min, appearing each time I played (four times for 5 minutes) the Boreal Owl staccato song (Bondrup-Nielson 1984). I finally had to suspend surveys to escape from these two curious birds. Their continued responsiveness suggested that naive juvenile Boreal Owls might be just as curious.

Less than a week later (19 August 1992) near Cumbres Pass on the New Mexico/Colorado border, I attracted a family group of two fledglings and one unidentified (probable adult) Boreal Owls with tape playback of the staccato song. The two young remained perched within 10 m for 25 min, offering ample time for careful examination of plumage characteristics. Subsequently, on 4 nights (28-29 July and 2-3 August 1993) of surveys with tape playback in northern New Mexico mountains, I attracted three Boreal Owls, one Northern Saw-whet Owl fledgling, and an unidentified *Aegolius* with tape playback. I saw two of the Boreal Owls; one was a fledgling accompanied by an unseen Boreal Owl. In total, six Boreal Owls, including three to four fledglings at two locations, responded to tape playback in 16 hours of systematic surveys in occupied Boreal Owl habitat. Locations of responding Boreal Owls were previously reported (Stahlecker and Duncan 1996).

A branching/fledgling Boreal Owl is distinctly plumaged; most of the body, including the facial disks, is chocolate brown, including both top and back of head (Mikkola 1983, Hayward and Hayward 1993). Primaries, secondaries, and wing coverts are brown with white spots, and the primaries are not molted until after reaching 1 year in age (Hornfeldt *et al.* 1988). Adults are streaked brown or gray on breast and belly with mostly white facial disks outlined in black. The top and back of the head are also black and flecked with smaller white spots than the wings and back (Mikkola 1983, Hayward and Hayward 1993). Neither intermediate plumages nor the molt rate are described.

Rawinski *et al.* (1993:57-58) described a southern Colorado Boreal Owl photographed on 2 September 1992 (fig. 1) as " 'subadult' because, unlike the adult plumage, this bird lacked the distinct black facial disk edge and also lacked the brown streaks on the breast. The breast was light brown to gray, and showed a downy appearance, suggesting a transition phase between the chocolate brown breast feathers of the juvenile and the streaked brown and white breast feathers of the adult."

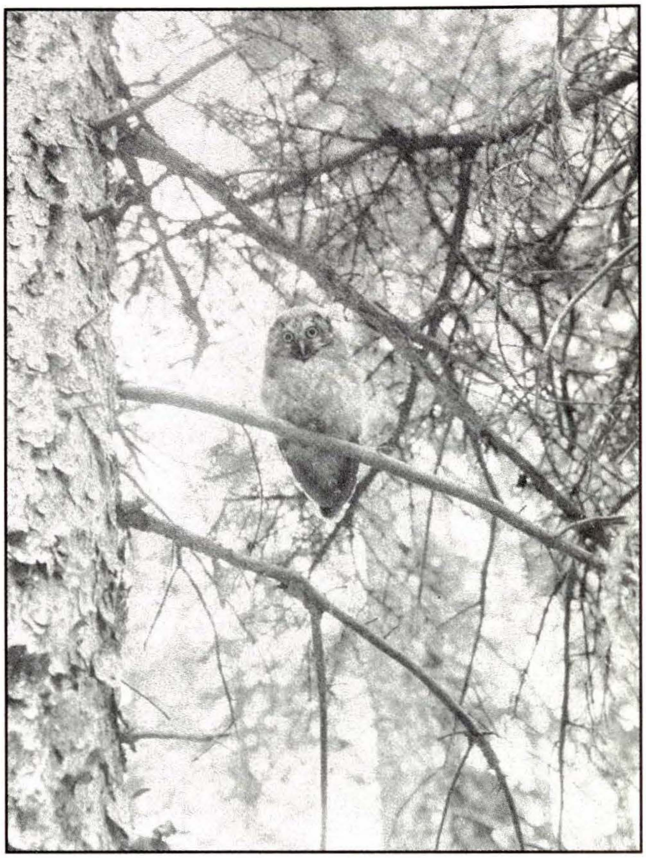

Figure 1.—*Post-fledging juvenile Boreal Owl* (Aegolius funereus) *near Creede, Colorado, 2 September 1992.*

The two young Boreal Owls that I observed on 19 August 1992 had streaked brown breasts and bellies, gray-black faces with distinct gray "lambchops" adjacent to the pale bill, and a clearly chocolate head and nape. One was also solid chocolate on throat and upper chest. The juvenile observed on 2 August 1993 was 8 m up in a tree. It did not have distinct facial disk borders, though disks were mostly white. Gray down protruded profusely from the head and upper body and the belly was streaked with brown and white. The nape and back of the head were not visible from directly below.

Northern Saw-whet Owls are also likely to respond to the Boreal Owl tape (Palmer and Rawinski 1986). In my experience, they are noticeably smaller, rustier in all plumages, and their "skiew" and "chuck" calls, though similar to those of Boreal Owls (Bondrup-Nielson 1984), are noticeably weaker than those of their congeners.

Tape playback in Boreal Owl surveys was initially used primarily during the breeding season (Hayward *et al.* 1987, 1993), but Palmer and Rawinski (1986) found that owls were also responsive during autumn (September-October). There is the added benefit that tape playback does not interfere with breeding activity (Palmer and Rawinski 1986). They recommended playing the staccato song for 5-min intervals from calling stations 200-800 m apart with two observers watching and listening for responding owls. Surveying with moonlight increased visibility of silent, flying owls and made backcountry travel easier. It was also important to call from a small clearing so that owls could approach closely from any direction, yet overflying owls could be seen against the moonlit sky. I recommend no change in that protocol, but suggest moving forward from autumn (September-October) into mid-summer (15 July -30 August) to increase the likelihood of attracting juveniles while they are still readily discernible from adults and still likely to be in the natal area. It may also be possible to attract the more easily identified chocolate brown fledglings even earlier in the summer (15 June-15 July), particularly at more southern locales, but I have not attempted systematic surveys that early.

Detection rates for singing Boreal Owls can vary year-to-year by up to several orders of magnitude (Hayward and Hayward 1993, Palmer 1987). Though it is not known how directly singing rates are correlated with nesting success, it seems logical that efforts to locate fledglings with this method would be most successful in years when the number of singing males in the region was high.

The most efficient means of locating Boreal Owl nests, with telemetry or through large nest box arrays, are expensive and time consuming. Hayward *et al.* (1992) reported material costs of $12-18/nest box and 220 person-hours/year to monitor 300 nest boxes with an average occupancy rate of 4.2 percent. Costs of telemetry studies are not reported. Agencies with time or budget constraints may not be able to devote the resources necessary to find active Boreal Owl nests. However, if they follow standardized protocol (Palmer and Rawinski 1986) for tape playback surveys and concentrate their efforts during mid-summer in areas already known to be occupied by Boreal Owls, recently fledged juveniles may be attracted within close range for identification and photographic documentation. This method may also be useful for documenting breeding locations for other species of owls.

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LITERATURE CITED

AOV [American Ornithologists' Union]. 1957. Checklist of North American birds. 5th ed. Baltimore, MD: American Ornithologists' Union.

Baldwin, P.H.; Koplin, J.R. 1966. The Boreal Owl as a Pleistocene relict in Colorado. Condor. 68: 299-300.

Batey, K.M.; Batey, H.; Buss, I.U. 1980. First Boreal Owl fledglings for Washington state. Murrelet. 61: 80.

Bondrup-Nielson, S. 1984. Vocalizations of the Boreal Owl, *Aegolius funereus richardsoni*, in North America. Canadian Field-Naturalist. 98: 191-197.

Hayward, G.D.; Garton, E.O. 1983. First nesting record for the Boreal Owl in Idaho. Condor. 85: 501.

Hayward, G.D.; Hayward, P.H. 1993. Boreal Owl. In: Poole, A.; Gill, F., eds. The birds of North America. Philadelphia, PA: The Academy of Natural Sciences and Washington, DC: The American Ornithologists' Union.

Hayward, G.D.; Hayward, P.H.; Garton, E.O. 1993. Ecology of Boreal Owls in the northern Rocky Mountains, U.S.A. Wildlife Monograph. 124: 1-59.

Hayward, G.D.; Steinhorst, R.K.; Hayward, P.H. 1992. Monitoring Boreal Owl populations with nest boxes: sample size and cost.

Journal of Wildlife Management. 56: 776-784.

Hayward, G.D.; Hayward, P.H.; Garton, E.O.; Escano, R. 1987. Revised breeding distribution of the Boreal Owl in the northern Rocky Mountains. Condor. 89: 431-432.

Hornfeldt, B.; Carlsson, B-G.; Nordstrom, A. 1988. Molt of primaries and age determination in Tengmalm's Owl (*Aegolius funereus*). Auk. 105: 783-789.

Korpimaki, E. 1984. Clutch size and breeding success of Tengmalm's Owl *Aegolius funereus* in natural cavities and nest-boxes. Ornis Fennica. 61: 80-83.

Mikkola, H. 1983. Owls of Europe. Vermillion, SD: Buteo Books.

Palmer, D.A. 1987. Annual, seasonal, and nightly variation in calling activity of Boreal and Northern Saw-whet Owls. In: Nero, R.W.; Clark, R.J.; Knapton, R.J.; Hamre, R.H., eds. Biology and conservation of northern forest owls; symposium proceedings; 1987 February 3-7; Winnipeg, Manitoba. Gen. Tech. Rep. RM-142. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 162-168.

Palmer, D.A.; Ryder, R.A. 1984. The first documented breeding of Boreal Owls in Colorado. Condor. 86: 215-217.

Palmer, D.A.; Rawinski, J.J. 1986. A technique for locating Boreal Owls in the fall in the Rocky Mountains. Colorado Field Ornithologist. 20: 38-41.

Rawinski, J.J.; Sell, R.; Metzger, P.; Kingery, H.; Kingery, U. 1993. Young Boreal Owls found in the San Juan Mountains, Colorado. Colorado Field Ornithologist. 27: 57-59.

Rogers, T.H. 1973. The nesting season: Northern Rocky Mountain-Intermountain Region. American Birds. 27: 895.

Ryder, R.A.; Palmer, D.A.; Rawinski, J.J. 1987. Distribution and status of the Boreal Owl in Colorado. In: Nero, R.W.; Clark, R.J.; Knapton, R.J.; Hamre, R.H., eds. Biology and conservation of northern forest owls; symposium proceedings; 1987 February 3-7; Winnipeg, Manitoba. Gen. Tech. Rep. RM-142. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 169-174.

Stahlecker, D.W.; Duncan, R.B. 1996. The Boreal Owl at the southern terminus of the Rocky Mountains: undocumented longtime resident or recent arrival? Condor. 98: 153-161.

Stahlecker, D.W.; Rawinski, J.R. 1990. First records for the Boreal Owl in New Mexico. Condor. 92: 517-519.

Whelton, B.D. 1989. Distribution of the Boreal Owl in eastern Washington and Oregon. Condor. 91: 712-716.

Landscape Features and Characteristics of Great Gray Owl (*Strix nebulosa*) Nests in Fragmented Landscapes of Central Alberta

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Abstract.—Forest fragmentation through timber harvesting, agricultural clearing, and other industrial activities is increasing on the Canadian landscape. This study was conducted in order to gain an understanding of habitat requirements for breeding Great Gray Owls (*Strix nebulosa*) in the forest fragments of central Alberta. I examined landscape and nest site characteristics around Great Gray Owl nests in these fragmented landscapes. Data were collected by owl banders who surveyed the study area by vehicle. When a Great Gray Owl was observed, the forest patch was searched until a nest site was located. Information on nest tree, vegetation, and nest type was recorded to identify basic characteristics of the forest fragment containing the nest. Using aerial photographs and a digital planimeter, the size of the forested fragments, the edge/area ratio, the distance from the nearest forest patch and the percent of forested land in a 1.15 km radius circle were measured. Similar information was collected from randomly selected areas to determine general habitat availability. Of 19 nests studied, all were located in mixed-wood forests; 17 nests were stick nests; two were in stumps. All nests were located in poplar trees (*Populus* spp.). Of the available habitat, there was a trend for owls to be located in larger forest patches, areas with a greater percent of forested area in the home range, and forest patches with less edge in relation to area. Although forest edge is an important component of Great Gray Owl habitat, it is evident that the amount of forested area adjacent to the edge is equally as important for the nesting of this species.

Industrial forest harvesting, clearing of forested land for agricultural purposes, and oil and gas exploration are activities that contribute to increasing the amount of fragmentation in Canada's boreal forest. Apart from the obvious structural change in the forest, very little is known about the avian communities that inhabit these newly created fragments and residual forest patches.

Studies have been conducted for owl species in fragmented landscapes (Redpath 1995); however, few projects have looked specifically at Great Gray Owl (*Strix nebulosa*) biology in fragmented northern forests. It is known that Great Gray Owls tend to nest in older, mixed-wood forests of Alberta (Oeming 1955); however, the landscape features of the nesting area are not well described. Several studies have suggested that certain features such as bogs and wetter areas are often associated with Great Gray Owls in the boreal forests of Canada (Duncan 1992, Harris 1984, Nero 1984), but this habitat association has never been documented in Alberta.

My objective was to summarize information obtained from several years of owl banding in Alberta, to characterize landscape features of owls in fragmented forests. The aims of this study were:

- To determine the minimum patch size used by Great Gray Owls in Central Alberta.

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- To measure landscape characteristics surrounding Great Gray Owl nesting areas.
- To test whether or not edge plays a significant role in habitat selection by Great Gray Owls.
- To identify the characteristics of Great Gray Owl nests in Alberta (forest type, nesting tree utilized, nest type).
- To measure the reproductive success of Great Gray Owls breeding in landscapes fragmented by agriculture.

METHODS

The data used in this study were obtained from the Alberta Natural Resources Service, incorporating Great Gray Owl nesting records that were recorded by banders in central Alberta between 1990 and 1995. The banders (Ray Cromie and Trevor Roper) annually conduct raptor surveys to locate hawk and owl nests, and compile this information for the Alberta Natural Resources Service.

The survey technique used by the banders to obtain this data involved driving along selected roads until a Great Gray Owl was observed. The roads were selected based upon their proximity to patches of fragmented forest. There was a selection bias towards older mixed-wood stands, as the banders preferred to survey roads adjacent to patches of older mixed-wood forests. The roads were driven between 1 to 15 times, with an average of 10 times for each road. Over 3,000 km were traveled between January and March each year. Roads in the survey were concentrated around Fort Saskatchewan, but covered areas as far north as Smith, as far south as Rocky Mountain House, as far east as Edson, and as far west as Lamont. All of the roads were located in central Alberta.

The survey area encompassed a variety of different agriculturally fragmented landscapes. These landscapes typically contained remnant patches of forests, scattered among cleared fields (used for grazing and agricultural crops) and towns. The forest patches in the area were largely composed of boreal forest vegetation, including *Picea mariana* (black spruce), *Picea glauca* (white spruce), *Populus balsamifera* (balsam poplar), and *Populus tremuloides* (trembling aspen) as the dominant tree species. When an owl was observed, its location was recorded on a map. If an owl, or a pair of owls, was detected at the same location more than once, or if an owl or pair of owls was recorded near a forest patch in March, the forest patch was searched intensively until a nest site was located. When a nest was found, its location was marked on a map and basic nest information (including legal land location, nest type, and nesting tree) was recorded. Nests were revisited to determine the reproductive success (determined by the number of chicks successfully reared to banding age).

Using aerial photographs of the nest areas, information was collected on landscape characteristics. The size of the woodland patch in which the nest was located was determined by tracing this patch with a digital planimeter (PLANIX 7, Tamaya & Company Ltd). Any barrier (road, water, buildings, clearing) was considered to be an obstruction to the forest, and the patch measurement did not extend beyond those barriers. To measure the amount of edge in relation to the size of the forest patch, the perimeter of the nest patch was measured and divided by the area of the patch. This was recorded as the edge/area ratio. The stand type was also interpreted from the aerial photograph as mixed-wood (a forest containing both *Picea* spp. and *Populus* spp.), pure coniferous (a forest consisting mostly of *Picea* spp.), or pure deciduous (a forest consisting mostly of *Populus* spp.) by using a stereoscope. An estimate of tree density within the stand was also estimated as less than 25 percent, 26-50 percent, 51-75 percent, or greater than 75 percent.

Other landscape characteristics were studied by looking at land features found within a 1.15 km radius of the center of the nest patch. A 1.15 km radius was selected based upon a description by Craighead and Craighead (1956) which suggested that Great Gray Owls travel over an area that can be as large as a circle 2.3 km diameter around the nest. Although this maximum range size from the Wyoming area is rather large, it is likely to be appropriate for the boreal forest of Alberta, as other northern owls (such as the Barred Owl, *Strix varia*) have been noted to have larger range sizes in Canada (James *et al.* 1995). Within this radius of the nest, the following features were recorded: number of other forest patches, sizes of other patches, proximity of other patches to the nest patch, and percentages of different land types (agriculturally cleared land, forested land, oil and gas, bogs, bare soil).

To compare the Great Gray Owl nest site locations with the available habitat, forest patches were selected randomly along the banders' transect routes. This was done by laying a numbered grid over the aerial photographs and using a randomly generated number to select a forest patch. The same data were collected for the nest patches.

The forest type and vegetation density of patches containing nests were compared to available habitat using a G-randomization test. The other landscape variables were compared using the Mann-Whitney U test. The values for edge/area ratio were tested for their correlation with the percent of forest in the home range by pairing the nest site values with the available habitat values that had the same percentage forest in the home range (Wilcoxon signed rank test). Non-parametric tests were used because of the non-normal distribution of the data.

RESULTS AND DISCUSSION

Landscape Features Associated with Great Gray Owl Nests

Bogs, oil and gas development, water, and buildings were detected at very low frequencies in the radius of both the nest sites and the randomly selected areas and were therefore not tested for in the statistical analysis. Studies of Great Gray Owl habitat in Manitoba (Duncan 1992, Nero 1980) and Saskatchewan (Harris 1984) have shown an apparent preference for nesting sites adjacent to muskeg or bog areas. No apparent association between Great Gray Owl nests and bogs or muskegs was found in central Alberta study area. This could be explained by the bias towards surveying mixed-wood stands; however, it is important to note that few bogs and muskegs were recorded in the available habitat (bogs were only detected in three of the randomly selected areas, and in these areas, composed less than 10 percent of the landscape). A more likely explanation is that bogs and muskegs were not associated with Great Gray Owl nests in central Alberta because they were not available in the area.

A possible theory that could explain why owls may be found near muskegs in some Canadian landscapes and in mixed-wood forests in other areas (such as in central Alberta) is the fact that Great Gray Owls require clearings for foraging. These clearings often can appear in the form of low growing shrubs (as seen in a muskeg) or in the form of grassy agriculturally cleared fields. The documented dependency of Great Gray Owls on muskegs may be overly specific. A more correct statement would be that Great Gray Owls are dependent upon clearings, which contain available small prey.

Numerous studies indicate that many owls are dependent upon prey availability for their continued survival and reproductive success (Adamick *et al.* 1978, Korpimaki 1984). The Great Gray Owl is no exception. Mice and voles make up a very large portion of the Great Gray Owl's diet (Bull *et al.* 1989a, Duncan 1992, Mikkola 1983, Oeming 1955). The habitat requirements of the common voles in Alberta (such as *Microtus pennsylvanicus*) are open, grassy meadows (Smith 1993). This explains why, in Alberta, nests of the Great Gray Owl are located in close proximity to clearings such as a grassy field created through agricultural fragmentation.

The size of the forest patch in which Great Gray Owl nests were located was significantly larger in size when compared to the available patches (table 1). In the areas where Great Gray Owls were found to occur, there were also significantly greater amounts of forested area, and larger forest patches adjacent to the actual nesting patch (table 1). In the agriculturally fragmented landscapes of central Alberta, Great Gray Owls appear to be found more frequently in larger patches of forest, surrounded by other forest patches. This is consistent with Great Gray Owls in Oregon, where nest sites were always located in forested areas (Bull and Henjum 1990).

Forest Edge

There was a trend for owls to be located in areas with lower edge/area ratios (P = 0.06, table 1). To isolate the effect of edge from overall amount of forest cover, edge/area of forest cover ratios for nest sites were paired with randomly selected areas of the same percentage forest cover. There was no significant difference (Wilcoxon; n = 17, z = -0.355, P = 0.72). This would indicate that the edge/area is highly correlated with the percentage of forest cover.

Table 1.—*Summary statistics of landscape features for forest patches containing Great Gray Owl (*Strix nebulosa*) nests and available habitat throughout the study area in central Alberta. Descriptive statistics (sample size, median, and range) are listed for each variable. Mann-Whitney tests were performed on the variables, and the results indicate that forest patch size, size of nearest forest patch, and percent of forested land in the owl's range were significantly different for the owl nest sites when compared with the available habitat (significance at P < 0.05).*

	Nest patch		Available habitat			
Variable	N	Median (Range)	N	Median (Range)	U test statistic	P-value
Forest patch size (ha)	19	29.6 (10.8-119.7)	38	17.8 (1.0-233.0)	482.5	0.04
Edge/area ratio for forest patches	19	81.7 (38.4-255.6)	38	107.4 (25.4-500.0)	250	0.06
Size of nearest forest patch (ha)	19	25.6 (5.6-280)	38	19.8 (0.0-145.0)	475.5	0.05
Distance from nearest forest patch (m)	19	40 (15.0-330.0)	35	40 (15.0-2580.0)	263	0.2
Percent of forested area in the home range	19	55 (17.0-95.0)	38	32.5 (5.0-90.0)	494.5	0.02

Great Gray Owls have often been considered an edge dependent species, as they mostly hunt in open areas adjacent to forest patches (Hilden and Helo 1981, Mikkola 1983, Winter 1986). Great Gray Owls show a preference for edge environments, which allows them to hunt in the cleared environments where their microtine prey is often found. In my study, the owls all nested in a fragmented environment where there was a great deal of edge produced by agricultural fragmentation. In addition to quantitative data, Great Gray Owls were visually recorded by the owl banders to be actively foraging on the edges of forest patches. These results suggest that in a fragmented environment, there is a preference for areas with a greater amount of forest area, thus having less edge. In an agricultural landscape, it is the forested area that is in demand, not the edges. Although further studies are necessary, I would speculate that this may be the reverse in a forested landscape, where edge is in demand, not the forest.

A possible explanation for the greater use of areas with less edge by Great Gray Owls in this study is that avian predators often take advantage of edge environments. Northern goshawks (*Accipiter gentilis*) and Great Horned Owls (*Bubo virginianus*) frequently prey on juvenile Great Gray Owls (Duncan 1987, Nero 1980). Logically, it would be to the benefit of the Great Gray Owl to select nest sites in forested areas with a minimal amount of edge.

Nest Characteristics

All of the nests were found in mixed-wood forests (N = 19), which was significantly different from the available habitat (68 percent mixed-wood, 18 percent pure coniferous, and 13.2 percent pure deciduous; $G_{ran} = 11.27$, $P = 0.002$). This observation is consistent with Oeming (1955), where mixed-wood poplar stands were noted to be the dominant forest type used by Great Gray Owls in Alberta.

All of the nests were located in poplar trees (*Populus* spp.), with 17 out of 19 nests in *P. tremuloides* and two in *P. balsamifera*. Of these 19 nest trees three were dead, and one was dead with a broken top, the rest of the trees were live (table 2). Of all nests, 17 were in stick nests and two were on stump nests (a nest located on the tree with a broken top).

Table 2.—*Summary of information collected on 19 Great Gray Owl (*Strix nebulosa*) nest sites in central Alberta from 1990-1995. The maximum, minimum, and mean number of chicks produced are summarized at the bottom of the table.*

Nest number	Nest * tree	Nest type	Chicks fledged
			Number
1	Bp	stick nest	2
2	Pt	stick nest	2
3	Pt	stick nest	3
4	Pt	stick nest	3
5	Pt	stick nest	3
6	Bp(broken top)	stick nest	3
7	Pt	stick nest	2
8	Pt	stick nest	2
9	Pt(dead)	stump nest	3
10	Pt	stick nest	2
11	Pt	stick nest	1
12	Pt	stick nest	3
13	Pt	stick nest	1
14	Pt(dead)	stump nest	3
15	Pt	stick nest	2
16	Pt(dead)	stick nest	3
17	Pt	stick nest	1
18	Pt	stick nest	2
19	Pt	stick nest	2
		Maximum	3
		Minimum	1
		Mean	2.26

* Two nest tree species were noted:
Bp - *Populus balsamifera*
Pt - *Populus tremuloides*

Tree density in the nest patches used by owls was greater than in the available landscape. All of the nests (N = 19) were found in forests with tree densities greater than 50 percent (31.6 percent were in forests of 51-75 percent densities, 68.4 percent were in forests of 76-100 percent densities), which was significantly different from the available habitat (26.3 percent in forest densities of 26-50 percent, 31.6 percent in densities of 51-75 percent, 42.1 percent in forests with densities of 76-100 percent; G_{ran} = 9.756, P = 0.01). In general, owls were often located in relatively dense mixed-wood stands which contained poplar trees with stick nests, stumps, or cavities suitable for nesting.

Reproductive Success

All 19 of the owl nests sampled produced young. The mean number of young fledged per nest was 2.3 (SD = 0.75), with a maximum of three chicks, and a minimum of one chick (table 2). This is consistent with studies in Oregon which had a mean number of young per successful nest of 2.3 (Bull *et al.* 1989b), and Finland which had 2.4 (Mikkola 1983). Reproductive success (as measured by the number of chicks fledged per nest) of Great Gray Owls in the agriculturally fragmented landscape of central Alberta does not seem to be measurably different from populations described elsewhere.

CONCLUSION

The effects of forest fragmentation on raptor species is poorly researched. Great Gray Owls are a species which require open areas for foraging, and thus forest fragmentation is seemingly a necessary landscape feature for this animal. However, in fragmented landscapes (such as central Alberta) the amount of edge available for foraging may not be as important as the amount of forested area available for nesting. As fragmentation of forests continues (e.g., by agricultural and timber industries), it will be increasingly important to ensure that mature forest patches are retained in the landscape for nesting of species such as the Great Gray Owl.

The status of the Great Gray Owl across North America is uncertain due to the lack of knowledge pertaining to this species (Hayward 1994). In Alberta, increasing pressure is being placed on forest raptors due to intense forest harvesting in the boreal forest. Industrial forest companies are attempting to manage forests based on ecological and wildlife principals (Weldwood 1990, Alberta Pacific Forest Products 1995), but without baseline biological data on key species such as the Great Gray Owl, it will be difficult to successfully implement and monitor management strategies. To conserve species such as the Great Gray Owl, a greater knowledge base must exist for this species. To maintain the species native to the boreal forests of North America, it will be essential for forest managers and researchers to share ideas and work together to implement management plans. Monitoring the long-term effects of different fragmentation patterns on wildlife species is a critical aspect of forest planning, if ecological and wildlife components are to be maintained.

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LITERATURE CITED

Adamcik, R.S.; Todd, A.W.; Keith, L.B. 1978. Demographic and dietary responses of Great Horned Owls during a snowshoe hare cycle. Canadian Field-Naturalist. 92(2): 156-166.

Alberta Pacific Forest Products. 1995. Boreal Ecosystem Management Forest. Edmonton Conference and Workshop.

Bull, E.L.; Henjum, M.G. 1990. Ecology of the Great Gray Owl. Gen. Tech. Rep. PNW-265. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Experiment Station.

Bull, E.L.; Henjum, M.G.; Rohweder, R.S. 1989a. Diet and optimal foraging of Great Gray Owls. Journal of Wildlife Management. 53: 47-50.

Bull, E.L.; Henjum, M.G.; Rohweder, R.S. 1989b. Reproduction and mortality of Great Gray Owls in Oregon. Northwest Science. 63: 38-48.

Craighead, J.J.; Craighead, F.C., Jr. 1956. Hawks, owls, and wildlife. Harisburg, PA: Stackpole Co., and Washington, DC: Wildlife Management Institute.

Duncan, J.R. 1987. Movement strategies, mortality, and behavior of radio-marked Great Gray Owls in southeastern Manitoba and northern Minnesota. In: Nero, R.W.; Clark, R.J.; Knapton, R.J.; Hamre, R.H., eds. Biology and conservation of northern forest owls: symposium proceedings; 1987 February 3-7; Winnipeg, Manitoba. Gen. Tech. Rep. RM-142. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 101-107.

Duncan, J.R. 1992. Influence of prey abundance and snow cover on Great Gray Owl breeding dispersal. Winnipeg, Manitoba, Canada: University of Manitoba. Ph.D. dissertation.

Harris, W.C. 1984. Great Gray Owls in Saskatchewan (1974-1983). Blue Jay. 43: 152-160

Hayward, G.D. 1994. Information needs: Great Gray Owls. In: Hayward, G.D.; Verner, J., eds. Flammulated, Boreal, and Great Gray Owls in the United States: a technical conservation assessment. Gen. Tech. Rep. RM-253. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station.

Hilden, O.; Helo, P. 1981. The Great Grey Owl *Strix nebulosa* - a bird of the northern taiga. Ornis Fennica. 58: 159-166

James, P.C.; Mazur, K.M.; Frith, S.D. 1995. The Barred Owl as an indicator of old forest and its role in long-term forestry planning. Prince Albert Model Forest Association Inc. Report.

Korpimaki, E. 1984. Population dynamics of birds of prey in relation to fluctuation in small mammal populations in western Finland. Annales Zoologici Fennici. 21: 287-293

Mikkola, H. 1983. Owls of Europe. Vermillion, SD: Buteo Books.

Nero, R.W. 1980. The Great Gray Owl: phantom of the northern forest. Washington, DC: Smithsonian Institute Press.

Nero, R.W.; Copland, W.R.; Mezibroski, J. 1984. The Great Gray Owl in Manitoba, 1968-83. Blue Jay. 42: 130-151.

Oeming, A.F. 1955. A preliminary study of the Great Gray Owl (*Scotiaptex nebulosa nebulosa* Forster) in Alberta, with observations on some other species of owls. Edmonton: University of Alberta. M.S. thesis.

Redpath S.M. 1995. Habitat fragmentation and the individual: Tawny Owls *(Strix aluco)* in woodland patches. Journal of Animal Ecology. 64: 652-661.

Smith, H.C. 1993. Alberta mammals; an atlas and guide. Edmonton, Alberta: The Provincial Museum of Alberta.

Weldwood of Canada Limited. 1990. Integrated management of timber and wildlife resources on the Weldwood Hinton Forest Management Agreement Area. Alberta Forestry, Lands and Wildlife.

Winter, J. 1986. Status, distribution and ecology of the Great Gray Owl (*Strix nebulosa*) in California. San Francisco, CA: San Franscisco State University. 121 p. M.A. thesis.

Workshops

WORKSHOP

Report on the Nocturnal Raptor Monitoring Workshop

Geoffrey L. Holroyd and Lisa Takats[1]

The goal of this workshop was to discuss the development of a strategy to determine the status and assess trends of nocturnal raptor species (i.e., nocturnal owls) in Canada and the USA. A strategy for diurnal raptor species was initiated at a workshop in Boise, Idaho in August 1996. The results of these workshops will form the basis for developing the North American Raptor Monitoring Strategy. This owl workshop focused on nocturnal survey techniques for inventorying and monitoring owls.

Another objective of this workshop was to review the efficiency and effectiveness of nocturnal owl survey techniques. Owl calling intensity varies throughout the year and may serve various functions. We discussed what we know about owl calling and our ability to survey owls at night. Playback calls are commonly used to survey owl populations. The workshop discussed the effectiveness, the time frames and species' responses to playback. Speakers analyzed their owl calling data to determine how owl calling varies within a wide variety of parameters including environmental conditions, owl behavior, observers, and techniques. Workshop participants then discussed how to contribute to the monitoring strategy.

BROADCAST SURVEYS AND MONITORING

Lisa Takats described some of the factors that affected owl detection in her 2-year study of owls in west-central Alberta. Her results are presented in a paper in these proceedings.

Glenn Proudfoot discussed the use of broadcast surveys to determine habitat use of Ferruginous Pygmy-owls (*Glaucidium brasilianum*) in southern Texas (these proceedings). Barbara and Jim Beck described the owl surveys they have conducted in central Alberta using playback techniques (these proceedings).

Frank Doyle, Department of Zoology, University of British Columbia, provided notes from an ecosystem study of cyclic fluctuations in predator-prey numbers in his study area adjacent to Kluane National Park in the southern Yukon. He compared the calling rates and the minimum number of male Boreal Owls (*Aegolius funereus*) in 1989-1996 and the known population of Great Horned Owls (*Bubo virginianus*) in 1989-1992 during peaks and lows of prey populations. The number of Great Horned Owls during a low in snowshoe hare abundance was 34 percent lower than in the peak of hare abundance, but the calling rate declined 81 percent. Likewise, but less extreme, when the number of Boreal Owls declined by 80 percent due to a low in vole abundance, the calling rate declined 87 percent. The abundance of prey also affected the onset of calling (calling started one month later in low food years), and the response rate (some males were not detected by playback in low food years). In addition, some owls flew towards the observer after playback, and then responded, providing false habitat data.

Pertti Saurola discussed the techniques used to monitor owls in Finland (paper in these proceedings). Of particular interest are the block study areas that volunteer ringers (banders) survey to determine nesting density of raptors, and in which they then band nestlings to provide a measure of productivity. Each year since 1982, 120 such blocks have been surveyed. Species of owl that are censused are Boreal, Long-eared (*Asio otus*), Ural (*Strix uralensis*), Eagle (*Bubo bubo*), and Pygmy-owls (*Glaucidium passerinum*). His data indicate that there is a 3-year cycle in owl numbers in Finland, with a cyclic low in 1984 and every third year since.

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RAPTOR MONITORING STRATEGY

Geoff Holroyd told the attendees about the workshop to develop a North American raptor monitoring strategy that was held in Boise, Idaho in August 1996. The goal of the North American Raptor Monitoring Strategy is to monitor the status and trends in continental and regional populations of Nearctic raptors in Canada, Mexico, and the USA. The strategy will present the optimum sampling design for surveys of each species of raptor, will critique sampling techniques and identify the species which currently lack suitable sampling techniques.

A report of the workshop discussion was produced in early 1997. The goal and objectives sections reads as follows: "The participants endorsed the need for a North American Raptor Monitoring Strategy. The goal of this strategy is to monitor the status and trends in continental and regional populations of Nearctic diurnal raptors in Canada, Mexico, and the USA. For the purposes of this strategy, diurnal raptors are defined as birds of prey in the taxonomic orders Falconiformes and Strigiformes whose primary activity pattern is diurnal."

The three objectives of this strategy are:

1. To monitor species to ensure that surveys have, at minimum, the ability to detect a 50 percent reduction in population size over a 25-year period with alpha = 0.10 and beta = 0.20; with the expectation that power to detect trends for the majority of species would be much greater.

2. To identify the best combination of monitoring techniques for each species.

3. To recommend improvements in data collection efforts, analysis methods, and regional coverage for each species and monitoring technique.

The table of contents includes these headings: Introduction, Migration Monitoring, Breeding Season Surveys, Non-Breeding Season and Wintering Surveys, Monitoring Strategy for Individual Species, Statistical Issues, Next Steps, Outline of the North American Raptor Monitoring Strategy, and Participant List. The workshop report is available at: http://www.im.nbs.gov/raptor/raptor.html, or from: Robert Lehman, U.S. Geological Service, Biological Resources Division, Snake River Field Station, 970 Lusk Street, Boise, ID 83706, USA. The monitoring strategy is being developed by a volunteer task force that communicates through a list serve. Interested parties can join the list serve by sending an E-mail message to: listproc@rana.im.nbs.gov
In the body of the message (not the subject line) put: subscribe raptrend <your name>.

The strategy will present the optimum sampling design for nocturnal surveys of each owl species, will critique sampling techniques and identify the species which currently lack suitable sampling techniques. The reader is encouraged to contribute to the development of the raptor strategy by discussing nocturnal counting methods, survey designs, coverage, analysis, and cooperation.

DISCUSSION

In this section we present the discussion of issues by members of the audience. One speaker noted that Dr. P. Beamish (1993. Dancing with Whales. Creative Publishers, St. Johns, Newfoundland) has found that the interval between sounds in whale calls is as important or more so for communication than is the actual sound. In response, another speaker noted that owls do respond differently to the same calls. The cadence and pitch of a call seemed to affect the owls' responsiveness. It was suggested that captive owls be used to better understand vocalizations, their meaning, the responses of the owls and the changes in the owls' behavior over seasons.

Christmas Bird Counts were discussed as a technique to monitor owl numbers, particularly peak numbers. However, they were criticized because the effort made to detect owls is not standardized. On many counts, owls are only encountered during daytime surveys. On a few counts, nocturnal surveys are conducted, but the amount and type of playback is not well documented in American Birds. It was suggested that there is a need to standardize Christmas Bird Count owling techniques so that the results could be comparable. Breeding Bird Surveys do not record many owls and appear to be ineffective for monitoring nocturnal owls.

One speaker felt that owling techniques and owl behavior were too variable to standardize over all of North America. He suggested a range of protocols should be tested and proposed, but the observer would determine the technique to be used at a given time and location. A standardized protocol was used to survey Spotted Owls but the technique was less effective over time possibly due to habituation of the owls, or changes in their responsiveness due to changing density and prey abundance. A response was that a starting point would be to count the number of owls that were calling spontaneously in the initial listening period as the standard. The length of this listening period should be optimized for the proportion of responses per minute. Four to 10 minutes seemed to be the range of initial listening periods. Once playback was initiated, more variation was introduced in the characteristics of the playback and the behavior response of the owls.

Other speakers expressed concern about the added stress to the owls that may be caused by playback. Smaller owls such as Saw-whet and Boreal will approach an observer who has played a tape, but not necessarily vocalize. Possibly the small owls are concerned about revealing their location to owl predators. Since we know little about the meaning of calls and how they change over time, listening silently is the least disruptive technique and is effective for most species. Regardless of the technique, one speaker reiterated that the number of calls is not a linear function of the number of owls present. At higher densities, owls spend more time calling, presumably to defend their territories from the increased number of owls that want to breed.

Overall, the participants supported the idea of a Nocturnal Owl Monitoring Strategy. The document will be a valuable tool that can be used, tested, and refined. Participants were encouraged to join the list serve and volunteer to help develop the strategy.

SUMMARY

Owl calling intensity varies throughout the year and may serve various functions. The use of playback calls is a commonly used technique but its effectiveness is unknown. Also unknown is each species' response to playback and how the responses vary with time, both through the night, seasonally, and during the reproductive season. Sampling owls at night is complicated by variations in owl behavior and environmental parameters which vary seasonally. Environmental parameters include: time of year, time of night, moon phase, and weather (temperature, wind speed, precipitation, barometric pressure, and pressure changes). Survey parameters include: playback calls (species, sequence, and length of time of playback); length of time listening (time of initial listening period, time between calls, and end time); volume of playback; tape recorder/speaker quality; and background noise interference. Owl parameters include: detection distance, inter-stop distance; owl movements/behavior in response to playback; variation in response to breeding cycle; and reaction of breeders to non-breeders. The responses are likely to vary geographically by latitude, longitude and season. Observer parameters include hearing ability of observers; disturbance of owls; roadside biases; and off-road options.

There are several opportunities for cooperation. Nocturnal playback surveys have been used in many projects. Current projects that involve volunteers are underway in Ontario, Alberta, Manitoba, and Montana. A cooperative effort by these and any other projects could result in a North American owl monitoring group. With the many variables associated with playback, one suggestion of workshop participants was that the owls recorded in the initial listening period should become the standard for monitoring. Any responses to playback should be treated separately. The initial listening period varies between surveys (3, 5, and 10 minutes are often used) and this should be standardized, possibly at 5 minutes. A technique similar to the Breeding Bird Survey could result.

ACKNOWLEDGMENTS

We thank all the speakers and members of the audience who participated in the discussion which we summarized above. Participants whom we were able to identify are: Barbara Beck, Michael Bradstreet, Steve Brechtel, Ray Cromie, Dick Dekker, Cam Finlay, Richard Fyfe, Denver Holt, Glenn Proudfoot, Pertti Saurola, Dale Stahlecker, and Troy Wellicome. Our apologies to those participants that we were not able to identify. Robert W. Nero kindly reviewed this paper.

WORKSHOP

Report on the Western Burrowing Owl (*Speotyto cunicularia*) Conservation Workshop

Geoffrey L. Holroyd[1] and Troy I. Wellicome[2]

This workshop was convened to review the current status of the Western Burrowing Owl (*Speotyto cunicularia hypugaea*) in North America, to discuss means by which we can improve our knowledge of this owl, and to initiate conservation action to benefit the species. About 70 people attended the workshop on the evening of 7 February 1997. Several speakers presented information on Burrowing Owls. Some of these speakers summarized information presented in earlier talks, as part of the Second International Owl Symposium, and others presented additional information relevant to the topic. Many people from the audience also contributed ideas and information. In this summary, we endeavor to present the main ideas that arose from the workshop and try to acknowledge each of the contributors. However, we apologize to those who may have been overlooked. We thank all those who participated in the workshop and who have since sent comments. We added new information about the trilateral agreement and decisions that became available in the spring of 1997 after the workshop.

The Burrowing Owl is an Endangered species in Canada and is declining rapidly; it is a Candidate 2 species and is declining in most of the western USA; and it has no designation in Mexico. In Canada, determination of the status of wildlife is made by the Committee On the Status of Endangered Wildlife In Canada (COSEWIC). In 1978, COSEWIC designated the Burrowing Owl as a Threatened Species, but in 1995 the designation was changed to Endangered (Wellicome and Haug 1995). In the USA, in 1994, the Burrowing Owl was listed as a Candidate 2 species. No public review of the species' status has been made since that time. In Mexico, the Burrowing Owl does not appear on any formal wildlife list.

Recovery efforts in Canada are coordinated through the Canadian Burrowing Owl Recovery Team, which has met each year since 1990. This team is comprised of researchers and representatives of wildlife agencies, but not of land-management agencies or industry associations. Its activities are guided by the Burrowing Owl Recovery Plan (Hjertaas *et al.* 1995).

STATUS IN CANADA

The first three speakers presented current information on the Burrowing Owl in Canada. Troy Wellicome, Department of Biological Sciences, University of Alberta, described the status of the Burrowing Owl in Canada on behalf of the Canadian Burrowing Owl Recovery Team, and outlined research he is conducting, in cooperation with Saskatchewan Fisheries and Wildlife, on "The effects of increased reproductive output on Burrowing Owl population change." The Burrowing Owl is declining across its Canadian range. There is only one pair left in Manitoba, down from 76 pairs 15 years ago, and only one pair known in B.C. despite a decade of reintroduction efforts after its extirpation there in 1979. Virtually all of the Canadian owl population is, therefore, now confined to southern Alberta and southern Saskatchewan, where there are less than 1,000 pairs remaining—down from more than 3,000 pairs in 1978. Declines in these two provinces average over 10 percent per year.

One of the factors implicated in the Burrowing Owl's decline is its seemingly low fledging rate. In Canada, this owl has an average clutch size of nine eggs but fledges only 3-5 young. Using food supplementation and predator exclusion, Troy and his colleagues have successfully increased fledgling output to high levels for 3 consecutive years. However, thus far, it is not clear whether increases in reproductive output can slow the owl decline in Canada.

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Kort Clayton, Department of Biology, University of Saskatchewan, discussed mortality of adults and young during the post-fledging period. Mortality of birds in the post-fledging period has been documented for 2 consecutive years near Hanna, Alberta, using radio-telemetry. Mortality of adult males was quite high between the time of fledging and fall dispersal (late-July to late-August), totaling 45 percent in 1995 and 35 percent in 1996; whereas, mortality was 0 percent for females during this same period in both years. Fledgling mortality was also quite high during this time: 65 percent in 1995 and 40 percent in 1996. There was, however, no mortality of adult birds or fledglings between fall dispersal and migration (late-August to mid-October) in either year. The majority of all post-fledging mortalities in Hanna resulted from avian predation.

Robert Warnock, Department of Biology, University of Regina, used data from the Operation Burrowing Owl program to test the hypothesized effects of landscape fragmentation on Saskatchewan's owl population. He found that the size of pasture fragments and the continuity of grassland habitat affects the distribution of breeding sites. The persistence of owl 'colonies' increased with higher habitat continuity, less patch edge, and more neighbor 'colonies'. Local extirpation from patches has increased and occupancy rates have decreased in Saskatchewan since 1987. He concluded that the remaining Burrowing Owl habitat in Saskatchewan appeared inadequate for population persistence.

STATUS IN THE UNITED STATES

In the western United States, the Burrowing Owl appears to be declining in most states where data exist, with the exceptions of parts of Colorado and Idaho. Several speakers discussed the status of the Burrowing Owl in the U.S. Bob Murphy, U.S. Fish and Wildlife Service, Des Lacs NWR Complex, North Dakota, stated that surveys in North Dakota in 1996 failed to find any Burrowing Owls where they had been found as recently as 1995 and where at least 90 historical breeding records existed. Dennis Flath, Montana Fish, Wildlife, and Parks, stated that relatively little information was available on the status of Burrowing Owls in Montana. However, he has access to early records of prairie dog colonies that occurred along the railroad right-of-way from 1907 to 1914. Based on those surveys, he has estimated that prairie dog colonies covered 1.5 million acres in eastern Montana. In the late 1980's, estimates of colonies in this area were as low as 180,000 acres, a decline of 88 percent. Recent publications suggest that prairie dogs now occupy only 2 percent of their former range in all of North America.

Dr. L. Trulio and Janis Buchanan described the desperate situation of Burrowing Owls in central California, where an informal working group has been working on Burrowing Owl conservation for several years. Despite their efforts, and with intensive land development in a region where land is worth over a million dollars per acre, the outlook for the Burrowing Owl is bleak. In several areas it is expected to be extirpated within 10 years.

Steve Sheffield, Clemson University, cautioned the audience that the Breeding Bird Survey and Christmas Bird Count data do not reflect a decline in western North America. However, small sample sizes and biases associated with these surveys make them of limited value for detecting declines for raptor populations. Geoff Holroyd pointed out that most of the winter records can be accounted for by Lubbock, Texas, where Burrowing Owls occur within a small, captive prairie dog colony.

MIGRATION AND WINTER

What do we know about Burrowing Owls on migration and during winter? Helen Trefry, Canadian Wildlife Service, Edmonton, Alberta, recently summarized all of the information on banding and band returns for Burrowing Owls in North America, and found that, of the thousands of birds banded in Canada, only a handful have been recovered in the U.S. and none in Mexico. None of the band returns for Canadian owls in the U.S. occurred during the winter months of November through March, but returns have been reported from as far south as south-central Texas and the Gulf Coast in both spring and fall. Migration from Canada occurs at night and begins in September, continuing through early October, and owls return between late March and mid-May. Habitats used during migration in the U.S. are unknown, but we assume the owls use burrows for cover in the daytime. Only 2 percent of prairie dog colonies remain, likely reducing the critical habitat available to owls on migration.

Geoff Holroyd summarized his surveys in northern Mexico, which were conducted in cooperation with PROFAUNA (Dr. Julio Carrera and his staff in Saltillo, Coahuila) since 1992; and in Texas in cooperation with Dr. Felipe Chauvez (Texas A&I University, Kingsville; and Kevin Mote, Texas Parks and Wildlife, Canyon) in January 1997. His field work indicates that the coastal lowlands of Texas and northeastern Mexico have a winter population of Burrowing Owls that are not present in summer. Also, Burrowing Owls appear more abundant in prairie dog colonies in northern Mexico in winter than in summer. Much of coastal Texas is cultivated and many Mexican black-tailed prairie dog colonies are vacant or cultivated.

A North American Burrowing Owl Conservation Program is needed to determine the status and conservation needs of the species in all three countries, and is a necessary component of Canadian recovery efforts. The Burrowing Owl's status in the USA and Mexico is unknown and needs to be determined. The extent of owl movement between the three countries and the association between breeding and wintering ranges need to be documented. Improved communication through formal and informal linkages will greatly facilitate status assessment and the performance of necessary conservation activities.

SOME RELATED MONITORING AND CONSERVATION INITIATIVES

Canadian Conservation Action

Operation Burrowing Owl (OBO) was created in 1987 in Saskatchewan and in 1989 in Alberta. OBO offers landowners the opportunity to aid in Burrowing Owl conservation by signing a voluntary agreement not to cultivate nesting habitat or use harmful pesticides in the area for 5 years. The agreements are renewed every fifth year. Over 700 landowners have signed agreements with Operation Burrowing Owl in Alberta and Saskatchewan to protect over 37,000 hectares (93,000 acres) of grassland habitat. Fragmentation due to previous cultivation of grassland may cause problems for the viability of breeding populations, but current loss of breeding habitat is less of a concern in Canada, since the number of owls is declining much faster than that the loss of native habitat. Many Operation Burrowing Owl landowners report that owls are not returning to previously-occupied and presently-protected habitat.

Trilateral Committee for Wildlife and Ecosystem Conservation and Management

This committee was established through an international memorandum of understanding, signed by the directors of the federal wildlife agencies of Mexico, Canada, and the United States on 9 April 1996. The purpose of the agreement is "to facilitate and enhance coordination, cooperation, and the development of partnerships among the wildlife agencies of the three countries, and with other associated and interested entities, regarding projects and programs for the conservation and management of wildlife, plants, biological diversity, and ecosystems of mutual interest.... Such projects and programs will include scientific research, law enforcement, sustainable use and any other aspect related to this purpose." At the second meeting of the committee in February, 1997 in Phoenix, Arizona, the committee established a working group to develop a continental approach to the conservation of Burrowing Owls. This working group will ensure international cooperation and communication to recover the Burrowing Owl.

Raptor Monitoring Strategy

Those who attended this workshop were told about another workshop, held in Boise, Idaho in August 1996, to develop a North American raptor monitoring strategy. Details of the workshop can be found in the paper on 'owl monitoring' by Holroyd and Takats in the present proceedings. The workshop report is available on the Internet at: http://www.im.nbs.gov/raptor/raptor.html or from Robert Lehman, U.S. Geological Service, Biological Resources Division, Snake River Field Station, 970 Lusk Street, Boise, ID 83706, USA. This monitoring strategy is being developed by a volunteer task-force that communicates through a list serve. Interested parties can join the list serve by sending an e-mail message to listproc@rana.im.nbs.gov
In the body of the message (not in the subject line) put 'subscribe raptrend <your name>'.

RECOMMENDED ACTIONS

The following actions were discussed at the Burrowing Owl workshop and were generally endorsed. However, there was no vote or procedure for 'democratic' input for these recommendations. Nevertheless, based on subsequent discussions, we are confident there is strong and broad support for these actions. We thank all participants for contributing to the success of this workshop.

1. An international working group be established to share information about the status of, and research on, the Burrowing Owl in North America, to define the conservation actions that could reverse its decline, and to coordinate cooperative implementation of recovery efforts.

2. An informal communication network be established. The network would likely consist of e-mail communication through an Internet 'list serve', a newsletter and a mailing list of interested researchers, conservationists, and others. Attendees signed-up for this network at the workshop.

3. A North American-wide survey of Burrowing Owls be conducted in 1998.

4. Where data exists on the distribution and abundance of Burrowing Owls, those areas be revisited in 1997 and/or 1998 to further document the trends in distribution and abundance of the owls.

5. A survey protocol be developed and distributed for use in the 1998 survey.

6. A major workshop on Burrowing Owl status, biology and conservation be held in Utah in autumn 1998, in conjunction with the annual meeting of the Raptor Research Foundation.

7. "Operation Burrowing Owl" land stewardship programs be implemented in the U.S. and Mexico to promote landowner stewardship and conservation of this species and its habitats. OBO will also provide valuable data on owl population trends, as it has done thus far in Canada.

8. The Burrowing Owl working group cooperate with any organization established to conserve prairie dogs. In particular, immediate action is needed to protect the few remaining colonies of Mexican black-tailed prairie dogs in Mexico.

ACKNOWLEDGMENT

We thank workshop participants for their input which we summarized above. Robert W. Nero kindly reviewed this paper.

LITERATURE CITED

Hjertaas, D.; Brechtel, S.; De Smet, K.; Dyer, O.; Haug, E.; Holroyd, G.L.; James, P.; Schmutz, J. 1995. National recovery plan for the Burrowing Owl. Recovery of Nationally Endangered Wildlife (RENEW) Rep. 13. Ottawa, ON: Canadian Wildlife Service. 33 p.

Wellicome, T.I.; Haug, E.A. 1995. Second update of status report on the Burrowing Owl (*Speotyto cunicularia*) in Canada. Ottawa, ON: COSEWIC, Environment Canada. 32 p.

WORKSHOP

The Role and Management Implications of Modeling Owl Populations and the Habitats They Occupy

Amy E. Kearns[1]

Abstract.—Modeling ecosystems is an evolving science that is both practical and theoretical. The integration of modeling, landscape ecology, management, and rapidly changing technology offers an array of possible solutions to modern environmental quandaries. In order to address these concerns, a workshop was developed to discuss the role and management implications of modeling owl populations and their habitats. The purpose of the workshop was to reflect on the previous symposium's biological, environmental, and management research; as well as how modeling has affected our understanding of owl management. The workshop focused on the roles that Geographical Information Systems, Habitat Suitability Index models, Meta-population models and Population Matrix models have played in owl management. The group developed a set of strategies for using these modeling techniques to promote ecosystem management.

Modeling ecosystems is an evolving science that is both practical and theoretical. The integration of modeling, landscape ecology, management and rapidly changing technology offers an array of possible solutions to modern environmental quandaries. According to Naveh and Lieberman (1994), the quantitative analysis of landscape heterogeneity, recent advances in computer hardware, remote sensing, geographical system information theory, hierarchy theory, percolation theory, fractal geometry, and model development are borne from an iterative process of model and field experiments. From the simplest linear model to the most complex stage-structured population matrix model, scientists and managers use models to understand ecosystems at many levels. Modeling can be viewed as a holistic approach to scientific research and used to conceptualize complex phenomenon, make comparisons and predictions, assess environmental impacts and optimize environmental decision making (Hall and Day 1977). Thus, ecosystems can be monitored to detect global change at varying scales. Models represent a set of choices among myriad techniques for understanding natural systems (Dunning *et al.* 1995, Turner *et al.* 1995).

Many owl biologists and managers believe the implementation of ecosystem management is at least a decade away. This workshop was designed to foster the development of a landscape and ecosystem approach to owl management by unifying prevalent ecological theories, applications and field research.

An earlier workshop (Haws 1987) focused on developing management plans for indicator species. The primary purpose of the present workshop was to reflect on the previous symposium's biological, environmental, and management research; as well as, how modeling has affected understanding of owl management. The specific objectives were:

1. to assess the role and management implications of modeling owl populations and their habitats;
2. to investigate past, present, and future modeling techniques for managing owl populations;

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3. to discuss the future of owl management and the importance modeling will have in owl management and;
4. to set goals that will foster the implementation of ecosystem management and landscape ecology principles into owl management.

WORKSHOP DESIGN

The workshop consisted of opening remarks from the chair (Amy E. Kearns) followed by four presentations concerning the use of Geographical Information Systems (GIS) in conjunction with models, Habitat Suitability Index models (HSI), Meta-population models, and Population Matrix models by: William Trowell, Manitoba Department of Natural Resources; James Beck, University of Alberta; Richard Gerhardt, Oregon; and Gregory Hayward, USDA Forest Service, Laramie, Wyoming. Each panelist presented information about a prevalent modeling technique available to owl biologists and managers at this time. The 2-1/2-hour workshop integrated presentations and discussion.

RESULTS

GIS and Modeling

GIS technology is having a profound impact on the way landscapes are being viewed in relation to resource use, particularly with respect to endangered and threatened species. The integration of GIS technology and modeling has the potential to promote a more holistic view of ecosystems. GIS not only serves as a reservoir for information, it can be used as a simulation tool and as an adaptive management resource. Many scientists and land managers are beginning to integrate GIS into modeling exercises to develop management strategies (Akcakaya *et al.* 1995; Akcakaya 1996; Lahaye *et al.* 1994). Lahaye *et al.* (1994) developed a simulation model for the California Spotted Owl (*Strix occidentalis occidentalis*) using GIS. The model integrates meta-population theory, population matrix models, GIS and has had a profound effect on California Spotted Owl management.

William Trowell demonstrated a GIS ArcInfo based program developed by Linnett Geomatics for the Manitoba Department of Natural Resources. The program is entitled Wildlife Habitat Assessment Modeling (WHAM) and is designed to integrate habitat suitability index models (HSI) and forest resource inventory data bases. Trowell used a Barred Owl (*Strix varia*) model to demonstrate the modeling program's capabilities. He began the demonstration by showing the participants a blank map of a township. Afterwards, he began to add thematic map layers and intersected these map layers with the HSI model. The resulting map and associated table conveyed the suitable habitat available to the Barred Owl within the township.

During Trowell's presentation, many people asked questions about the program's ability to incorporate spatio-temporal parameters into the model. In particular, the participants were interested in the program's ability to recognize the interaction between different habitat types. Currently, WHAM is unable to perform these sorts of analyses; however, these capabilities can be built into the GIS ArcInfo program.

Habitat Models

Dr. James Beck presented information about habitat modeling, in particular HSI models. He conveyed the importance of validating models and presented some information about field testing models. HSI models have evolved from the Habitat Evaluation Program which was designed to address the need for modeling the interaction between animals and the habitats they occupy. In the past, these models were developed by consulting literature and by using baseline field data. Many of these HSI models have received limited validation resulting in the model's limited applicability. The main purpose of these models has been to set interim forest management recommendations. Beck emphasized the need to develop models using information collected in the field.

The most critical decision that must be made when developing HSI models is deciding which variables to include and exclude from the model. The discussion group agreed that more emphasis should be placed on incorporating less resource-based variables and more universal habitat component variables. These models attempt to retain the essential elements of quality wildlife habitat for a particular animal; however, they can be oversimplified and coarse grain. Beck emphasized this point by showing an image of an owl fashioned from letters, dashes and numbers commonly found on a keyboard. This image was used as an analogy between HSI models and reality. Even though the image retained all of the essential elements of an owl, the finer details of the owl were not included.

Many suggestions were made for improving habitat suitability models, e.g., incorporation of spatial and temporal dynamics into the models. Turner *et al.* (1995) stated that habitat suitability models have attempted to prescribe the range of habitat conditions that will provide the requirements for a particular species; however, these models do not incorporate spatial dynamics. The group also suggested including more detailed information about the interaction between populations and measurements of reproductive fitness.

Meta-population Models

Dr. Richard Gerhardt presented information about the progress that has occurred over the last 10 years with respect to meta-population research and theory. An enormous amount of interest in the dynamics of meta-populations has emerged over this time period (Mangel and Tier 1993). He began the presentation by defining the terminology associated with meta-population analysis and demonstrated the need to integrate the theories associated with meta-population analysis into field research. Gerhardt emphasized the connection between meta-populations and habitat. One of the central factors influencing movement between populations is the surrounding habitat. The amount of suitable habitat present within a given area greatly influences the cycle between local population extinctions and colonizations and persistence of a species over a broad landscape. Dytham (1995) described one model that incorporated a two-way interspecific competition between two organisms and their presence in the landscape.

Genetics is an important tool for monitoring movement of individuals among populations. By investigating the meta-population concepts in the field, information concerning the movement of individuals between populations and how habitat characteristics influence these movements can be examined.

Modeling these interactions can improve understanding of the ecosystems occupied by owls.

Population Matrix Models

Dr. Gregory Hayward introduced the topic of population matrix models. The Leslie matrix and some measure of fitness (λ) form the basis of these models. Once demographic data have been collected, they are organized into a population matrix. These matrices can be organized into an age-structured model or a stage-structured model. Accurate information about the age structure of a given population is necessary for developing an age-structured model; whereas, stage-structured models are more flexible and can utilize a wider variety of information. Stage-structured models are concerned with such parameters as density dependence, senescence and reproductive change over time. A more in-depth discussion can be found in Hayward and McDonald (1997) in this proceedings.

Dr. Hayward described how these models could be used to design efficient field protocols. Dunning *et al.* (1995) suggested using population simulation models to study population dynamics in heterogeneous landscapes. For a more in-depth discussion of Hayward's presentation see Hayward and McDonald (1997) in this proceedings.

CONCLUSIONS AND RECOMMENDATIONS

The primary recommendation developed from the workshop was support for the integration of population models and habitat suitability models. Participants suggested HSI models should incorporate some measure of fitness. By incorporating reproductive fitness into the equation, a more realistic depiction of the relationship is possible. Another suggestion made was to incorporate spatial and temporal variation and interactions into habitat models. These models should be designed to answer questions about how different habitat attributes interact and work synergistically to affect animal populations. According to Holt *et al.* (1995) this will involve the judicious meshing of different spatial and temporal scales. Kareiva and Wennergren (1995) agree that one of the critical tests of ecological sciences will be to see if scientists can profitably use insights from these spatially explicit models to solve practical problems facing biologists today. Future discussion should emphasize investigating the possibility of using fractals to remedy problems associated with scaling problems.

The discussion group recognized the need to communicate the results of modeling to the public. The group recommended that model developers should work on making their models understandable and useful to mathematicians, theoretical ecologist, wildlife managers, biologists, and the general public alike.

LITERATURE CITED

Akcakaya, H.R. 1996. Linking metapopula-tion models with GIS for population viability analysis: conserving species dependent on older forests: a population viability assessment workshop. In: Flemming, S., ed. Ecosystem Science Review Reports. Parks Canada: 1-12.

Akcakaya, H.R.; McCarthy, M.A.; Pearce, J.L. 1995. Linking landscape data with population viability analysis: management options for the Helmeted Honeyeater *Lichenostomus melanops cassidix*. Biological Conservation. 73: 169-176.

Dunning, J.B.; Stewart, D.J.; Danielson, B.J.; Noon, B.R.; Root, T.L.; Lamberson, R.H.; Stevens, E.E. 1995. Spatially explicit population models: current forms and future uses. Ecological Applications. 5(1): 3-11.

Dytham, C. 1995. The effect of habitat destruction pattern on species persistence: a cellular model. Oikos. 74: 340-344.

Hall, C.A.; Day, J.W., Jr. 1977. Ecosystem modeling in theory and practice: an introduction with case histories. New York, NY: Wiley-Interscience Publications.

Haws, K. 1987. Owl management techniques. In: Nero, R.W.; Clark, R.J.; Knapton, R.J.; Hamre, R.H., eds. Biology and conservation of northern forest owls: symposium proceedings; 1987 February 3-7; Winnipeg, MB. Gen. Tech. Rep. RM-142. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 302-304.

Hayward, G.D.; McDonald, D. 1997. Matrix population models as a tool in development of habitat models. In: Duncan, J.R.; Johnson, D.H.; Nicholls, T.H., eds. Biology and conservation of owls of the northern hemisphere: 2d international symposium; 1997 February 5-9; Winnipeg, MB. Gen. Tech. Rep. NC-190. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station: 205-212.

Holt, R.D.; Pacala, S.W.; Smith, T.W.; Liu, J. 1995. Linking contemporary vegetation models with spatially explicit animal population models. Ecological Applications. 5(1): 20-27.

Kareiva, P.; Wennergren, U. 1995. Connecting landscape pattern to ecosystem and population processes. Nature. 373(26): 299-302.

Lahaye, W.; Gutierrez, R.J.; Akcakaya, H.R. 1994. Spotted Owl metapopulation dynamics in Southern California. Journal of Animal Ecology. 63: 775-785.

Mangel, M.; Tier, C. 1993. Dynamics of metapopulations with demographic stochasticity and environmental catastrophe. Theoretical Population Biology. 44: 1-31.

Naveh, Z.; Lieberman, A.S. 1994. Landscape ecology: theory and application. 2d ed. New York, NY: Springer-Verlag. 360 p.

Turner, M.G.; Arthaud, G.J.; Engstrom, R.T.; Heil, S.J.; Liu, J.; Loeb, S.; McKelvey, K. 1995. Usefulness of spatial explicit population models in land management. Ecological Applications. 5(1): 12-16.

WORKSHOP

"Mission Possible: Owls in Education"

Marcia J. Wilson[1]

Abstract.—A panel of four experts in the fields of environmental education, rehabilitation and research assembled for a 1-3/4 hour workshop chaired by a moderator. Each panelist reflected upon their experiences using live owls in their own environmental education and/or research programs. Permanently disabled or imprinted owls can live long, useful lives as ambassadors from the world of wildlife. Given proper handling, training and care, these owls provide a compelling connection to the natural world for both children and adults. Likewise, an up-close and personal encounter with a wild owl can open minds of any age to the broader issues of conservation. Discussion of the agenda topics among the panelists, moderator and 74 workshop attendees was lively and stimulating. Attendees commented and asked questions. Discussion topics included program descriptions, teaching and handling techniques, ethics, cosmetics of non-releaseable owls, communication between educators and researchers, the virtues of owl pellets as teaching tools and issues regarding their sources, travel techniques, and use of the Internet among educators, students and researchers. A live Great Horned Owl (*Bubo virginianus*) was present to help illustrate topics discussed during the workshop.

Moderator Marcia Wilson (Ms. Wilson) opened the workshop by reading from the journal of naturalist Henry David Thoreau:

> "Jan. 7. [1854] P.M. - To Ministerial Swamp. I went to these woods partly to hear an owl, but did not; but now that I have left them nearly a mile behind, I hear one distinctly, *hoorer hoo* [imitates Great Horned Owl call]. Strange that we should hear this sound so often, loud and far,—a voice which we call the owl,— and yet so rarely see the bird. Oftenest at twilight. It has a singular prominence as a sound; is louder than the voice of a dear friend. Yet we see the friend perhaps daily and the owl but a few times in our lives. It is a sound which the wood or the horizon makes." (Cruickshank 1964).

This passage embodies most people's experience with owls, as they are more often heard than seen. People remember their experiences with owls in great detail and regard the birds as rare, special, and even magical.

Ms. Wilson introduced herself and each of the panelists by reading biographical sketches (see below). Before the panelists presented their own opening statements, Ms. Wilson acknowledged the assistance and inspiration of Dr. Bob Nero, educator, biologist and a key member of the Owl Symposium Committee; Dr. Jim Duncan, chairman of the Owl Symposium Committee; Ms. Kay McKeever, director of The Owl Foundation; Mr. Mark Wilson, wildlife photographer, writer, and Ms. Wilson's husband; and Mr. Denver Holt, wildlife biologist and president of the Owl Research Institute,

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[1] Marcia J. Wilson, Workshop Moderator and Director of Eyes On Owls live owl programs, P.O. Box 220, Dunstable, Massachusetts, 01827-0220, U.S.A.

Missoula, Montana. Ms. Wilson also introduced Lisa Braun (Ms. Braun) of the rehabilitation staff at the Manitoba Wildlife Rehabilitation Organization (MWRO) in Glenlea, Manitoba. Ms. Braun kindly brought a live Great Horned Owl from MWRO and positioned the owl on a free-standing perch to the left of the panelists. Ms. Kim Middleton, a volunteer at MWRO, accompanied Ms. Braun and assisted with transport and set-up of the owl.

PANELISTS

1. Shawna Wiebe (Ms. Wiebe), Rehabilitation Director (formerly), Manitoba Wildlife Rehabilitation Organization (MWRO, Box 49, Glenlea, Manitoba, R0G 0S0) 137 Le Maire Street, Winnipeg, MB, R3V 1E1; (204) 883-2122 MWRO; (204) 261-8395, fax (204) 883-2582. As Rehabilitation Director, Ms. Wiebe ran MWRO's wildlife hospital until 1 February 1997, working closely with the education program, coordinating volunteers and training, and overseeing media coverage. She also trains dogs in obedience and search and rescue. She holds bachelor's degrees in both science and education.

2. Rick Smith (Mr. R. Smith), Elementary School Teacher, Queenston School, 245 Queenston Street, Winnipeg, Manitoba, R3N 0W6; (204) 489-3423, fax (204) 488-6639. Experienced at teaching various grade levels, Mr. Smith has focused for the past 6 years on actively involving elementary school children in science, often using live animals. He has a passion for sixth graders. Lady Grayl, Dr. Robert Nero's captive Great Gray Owl (*Strix nebulosa*), is no stranger to his classroom. He uses science fairs and clubs to generate interest among students. Under Mr. Smith's guidance, students raised money for the Manitoba Wildlife Rehabilitation Organization. He holds a bachelor's degree in education.

3. Katy Duffy (Ms. Duffy), Assistant District Naturalist at Grand Teton National Park, Moose, Wyoming, USA 83012; (307) 739-3593, and Owl Researcher at Cape May, New Jersey. Using mounted birds, study skins and parts (feet, wings, tails, skulls, pellets), Ms. Duffy has presented programs on owls and hawks for general park visitors, special adult groups and children for the past 14 years. She is a Saw-whet Owl (*Aegolius acadicus*) researcher and bird bander. Ms. Duffy has conducted an owl banding project each fall since 1980 at Cape May, New Jersey. She does demonstrations with live owls and other birds during her banding studies and has encouraged public participation in her research projects. She holds an undergraduate degree in biology and a master's degree in ecology.

4. Norman Smith (Mr. N. Smith), Director, Educator and Owl Researcher at Blue Hills Trailside Museum and Chickatawbut Education Center, 1904 Canton Avenue, Milton, Massachusetts, USA, 02186; (617) 333-0690, fax (617) 333-0814. Mr. Smith brings 27 years of raptor study to his educational programs presented both at the museum and in metropolitan Boston schools. His experience with hawks and owls includes 20 years of rehabilitation and bird banding. A self-taught naturalist, he has worked for the Massachusetts Audubon Society (MAS) for 23 years, currently serving as natural history museum director. Mr. Smith studies wintering Snowy Owls (*Nyctea scandiaca*) at Boston's Logan Airport through a long-term color-marking, banding and relocation project. He and his two children are featured in *"Owls Up Close"*, and *"Hawks Up Close"*, videos produced for the National Audubon Society by the Nature Science Network.

5. Marcia J. Wilson, Workshop Moderator and Director of Eyes On Owls live owl programs, P.O. Box 220, Dunstable, Massachusetts, USA, 01827; (508) 649-3779, fax (508) 649-7377. With over 30 years of experience in biology, field ornithology and environmental education, Ms. Wilson presents live owl programs to schools and adult groups throughout eastern Massachusetts and southern New Hampshire. Her presentations feature owl photos taken by her husband, wildlife photographer Mark Wilson. Born to birding parents, she had the good fortune to grow up with owls as her mother presented live owl programs to schools. Ms. Wilson now devotes her time to teaching about owls. Ms. Wilson holds a bachelor's degree in biology.

AGENDA

1. Educational Programs: What works? What doesn't? Panelists share innovative tips and techniques for outreach. Education is more than just an owl on a fist.
2. Owls Up Close: How are owls presented to the public? Panelists discuss ethics of anthromorphism, handling techniques and cosmetics. Can an owl's disabilities detract from the educational message?
3. Teaching the Teachers: How do educators and rehabilitators keep abreast of current research on owls? Newsletters, scientific journals, magazines, cyberspace, conferences: are these the best sources for information?
4. A Pellet Primer: Do commercial supply companies impact wild owl populations as they fill bulk orders for pellets for schools? Are there alternative sources?
5. Owls on the Road: What special challenges do the birds face during time away from their accustomed enclosures? Issues of stress, dehydration, feather wear, travel techniques, rest, and feeding will be explored.
6. Owls on Line: How are teachers, students, and researchers interacting through the Internet? How do we inspire kids to look beyond their computer screens and explore the natural world?

PANELISTS' INTRODUCTORY REMARKS

Ms. Wiebe: As former rehabilitation director of MWRO, Ms. Wiebe described taking educational programs on the road to classrooms and mixed age events with children and adults. Her programs focused on interactions of people with the natural environment, stressing conservation and preservation of natural habitats and wildlife. She also explained how some well-intentioned human interactions at times, in fact, created non-releasable birds.

Mr. R. Smith: As one who has taught a wide range of students in Winnipeg's public schools, Smith spoke of embracing the study of owls in his curriculum. After an intensive period where students learn about owls' biology, life cycles, and habitat needs, Mr. R. Smith uses a live owl presentation, often by Dr. Nero with his captive Great Gray Owl, "Lady Grayl", as well as field trips to round out their learning about owls. He uses these interactive experiences to get students interested in science.

Ms. Duffy: In speaking of her natural history presentations and field trips at Grand Teton National Park, and during her Saw-whet Owl banding research at Cape May, New Jersey each fall, Ms. Duffy emphasized the impact of sensory and tactile impressions on all who participate in her programs. She strives to involve everybody with owls through her own solid knowledge and an infectious enthusiasm for her work. Ms. Duffy has observed that people will only protect what they know and love.

Mr. N. Smith: Painting a scene of his own childhood experiences with owls, Mr. N. Smith described how many of his friends thought he was "really wierd." His parents' friends expressed reservations when he ventured with their sons to a nearby coastal barrier beach with the family car to look for Snowy Owls. The Smiths explained that, "no, their sons weren't going out for a few drinks, but really *were* out looking for owls." Shortly after that, Mr. N. Smith began working for the Massachusetts Audubon Society doing environmental education programs which now, some 25 years later, reach 400,000 people near a major metropolitan city, Boston. He spoke of the heartening experience of opening the eyes of inner city children to the world of wildlife, forests, and whole ecosystems, as a contrast to their daily lives where single trees, asphalt, gangs, and violence are the mainstays of their environment. MAS's Trailside Museum now operates hawk and owl banding stations at two locations, in addition to Mr. N. Smith's Snowy Owl project, where students are incorporated into various research projects.

After Mr. N. Smith began involving his own two children, to whom he referred as his "assistants", with his Snowy Owl research at Logan Airport in Boston, he realized the critical value of involving children in hands-on environmental education and research projects. "One day at last light", he related, "one of my assistants, then aged 7, insisted we try to trap a Snowy Owl perched in a tree about 2 miles away. Even with 50-power binoculars, we weren't even sure it was an owl. After explaining to her that I was the researcher who had read 117 research papers on Snowy Owls, that owls' vision had no magnification ability, and that trying to trap the bird was really a waste of time, she looked up and said, 'Dad, I think you're making a big mistake because this may be a bird that you may've caught in the past, and this could be a real interesting situation.' So I said, 'OK. To show my assistant how wrong you are, we will take this trap, put it out on the edge of a runway, with brown grass. We will put a starling in the trap and wait 5 minutes. It's getting late, downtown Boston traffic is horrendous, we told Mom we'd be home at 6 o'clock, it's 5:30 now, she's going to be really upset, but we'll give it 5 minutes.' So we put the trap out, and just to show her how wrong she was, within about 2 minutes we saw this big white thing coming in, flying across the water, and landing on that starling. So she looks up at me and says, 'So, Dad. You know how well Snowy Owls can see.' And from that point on, I realized maybe we don't know as much as we think we know about these creatures. By stimulating and inspiring young children who have a lot of ideas, and don't get shut off or put off by these things because they think someone knows, in fact, maybe it's really right."

In an aside, Mr. N. Smith shared some highlights of his Snowy Owl banding work at Logan Airport, Boston. When he first began 15 years ago, researchers believed Snowy Owls were coming to Massachusetts in the winter starving to death due to low food resources in the North. In fact, during big flight years, he found most owls were in excellent condition. Ninety percent of them were young birds. They had very few parasites. Their plumage was perfect. In non-flight years when there were few Snowy Owls, he found they were mostly adult birds, emaciated, had poor feather condition, and were loaded with parasites. Correlating this with what was happening in the Arctic tundra, he found that in years when there were plenty of lemmings, lots of young Snowy Owls were produced. So, there were lots of healthy birds to disperse southward. Researchers had also believed that these owls never returned to the Arctic. Mr. N. Smith has captured 10 banded Snowy Owls that have returned to Logan Airport, and thinks other banded owls return that he's unable to capture. Two weeks before the symposium, he caught an owl he'd banded 10 years ago. So he believes some of these birds do return. He said researchers still have no idea exactly where they go to or where they come from.

In closing, Mr. N. Smith affirmed a belief common to all four panelists: "To me, it's a lifelong mission to instill education in people, because even everyone in this room, even the little you think you know, can be really important to somebody else."

Ms. Braun gave a brief background on the Great Horned Owl present at the workshop. A farmer found a dead adult Great Horned in barbed wire not far from the nest. After waiting a couple of days, he cut the tree down to get the young owls. This owl suffered from head trauma and its sibling died. The farmer kept the owl another 2 weeks, during which time the trauma was set and the bird became imprinted on people at this critical young age. After it was brought to MWRO, the owl was found to be blind in its left eye and deaf in its left ear, rendering it non-releaseable. The owl, a cosmetically beautiful, light-plumaged female, is now used for educational programs by MWRO.

DISCUSSION

Since each of the panelists had already touched on agenda question #1 about individual approaches and techniques in their own educational programs, Ms. Wilson continued with a formal discussion of the agenda. She asked them to comment on ethical questions, such as how the bird is being handled and presented, and what the group's perception is. She posed, "Is it being treated as a pet? Is it being regarded as a wild bird? I'm sure we've all in this room seen live animal programs that are presented in a fashion that the animal's really being treated as a house pet, even though it might be a wild species. So let's reflect a little bit on that issue. I know that Norman, you have some views on that with regards to your presentations at the museum, so that certain perceptions are upheld. Perhaps you could reflect on that for us."

Mr. N. Smith: Non-releaseable live owls, other birds and animals are utilized at Blue Hills Trailside Museum. Historically, it has been a real drawing card to offer people the chance to see a wild animal up close, because it attracts their attention and gives educators a chance to hopefully get an educational message across to them. To illustrate how presentation techniques have evolved at the Museum, Mr. N. Smith gave an example of how years ago a striped skunk, "Sandy the skunk", was held in front of a group and presented as a wild animal, all the while being petted by the well-meaning teacher-naturalist. Although the message was that people shouldn't keep skunks as pets, Mr. N. Smith stressed, "as we all know, particularly young kids don't hear with their ears, they hear with their eyes. When they see Sandy the skunk being petted, they think, 'Ya. I would like to have a pet skunk myself.' Why not?" The children all lined up after the program to touch the skunk. Some time later, a mother called the museum to say her daughter was really thrilled to meet Sandy the skunk, but while on a family picnic, the little girl mistook a "tame" skunk with distemper and tried to pet it. Now, Mr. N. Smith explained, the museum does not give its birds or animals names, he presents them on perches, tables, or natural exhibits, and instead of petting the animal, people get to hold wings, bones or preserved specimens. He firmly believes there are valuable benefits to being able to see wild animals, such as the Great Horned Owl at the workshop, up close and be able to learn about their important features.

Ms. Wilson: Mr. R. Smith, having worked directly with many different ages of children as a public school teacher, was asked, "How do you instill a respect for a wild animal in your students and what are some of their reactions when, specifically, live owls are brought in?"

Mr. R. Smith: Working with grades 4, 5, and 6, he finds that most students have never seen a wild owl up close. His students sponsored Dr. Bob Nero's program where he brings Lady Grayl, an imprinted Great Gray Owl, into the classroom. He's found that some children are timid or shy around the owl because it is wild, and adults will react this way, too. On the other end of the spectrum, he's seen children and adults who really want to touch the owl. His students donated money raised for Dr. Nero's Lady Grayl Fund to MWRO. Although MWRO is not normally open for group visits, Mr. R. Smith's students were allowed to visit the facility. There were some birds they were not allowed to see up close to prevent imprinting, and that concept was a lesson of its own to the students. He said, "Live animals are always a nice hook or a nice prompt for kids. I never have any problem getting my kids interested in research or in owls."

Mr. R. Smith showed some poster displays about owls his students had made. Two of his students had spotted and correctly identified a Great Gray Owl earlier this winter and had photographed it in River Heights, within Winnipeg city limits. "I think that's the part of the impact of education that you can't really measure. Who's to know that these guys were ever to see an owl again and recognize it?"

Ms. Wilson: "Now Katy, when you're handling all of those Saw-whets in New Jersey, and you have all those little kids around you, what do you do? Do you allow the kids to touch the birds?"

Ms. Duffy: "I do let people touch the owl. I show them that I'm handling them gently, but firmly, and explain why. To me the supreme honor if you're a visitor to my owl banding project is for me to let you release a Saw-whet Owl. We go outside, shut off all the lights, and release the owl at my usual spot. I'm a firm believer that a bird in the hand is best." At this very moment, the live Great Horned Owl gives a full 4-note hoot. "So, is that approval?" (Everyone laughs) Ms. Duffy discourages petting the owls, yet allows the group to feel how soft the feathers are, how large the skull is, etc. while handling the bird gently. She explains that the owl is perfectly capable of scratching and biting if not handled carefully, and added that people are thrilled with the experience.

Ms. Wilson: "Now that's a really fun example of how she's using bird banding to allow people to touch the bird, because they *all* want to touch the bird. My parents are bird banders, and as a child, I can't tell you how thrilling it was to be able to hold and release a bird." She explained that legally in the U.S. educators are discouraged from letting people touch the bird from a liability standpoint and to protect the birds. Yet, by letting someone release a banded bird, a researcher can provide a lasting memory for a child or adult. She next asked how Ms. Wiebe responds to the question from children, "I want to have an owl when I get older. Where do I buy an owl?"

Ms. Wiebe: Ms. Wiebe tends to get questions like this more often when the owl is displayed on the fist than on a stationary perch. People tend to associate the bird's behavior with its handler, and often remark that the owl seems to "like" the person. She explains that the birds are wild animals and don't show affection. The birds cannot survive on their own in the wild because of their disabilities. She emphasizes respect when questions like, "Can I pet it? Can you pet it?" come up, adding that the owls are not pets like budgies. The wild owl has its space and they try not to invade that space. She uses the concept of predator-prey relationships to explain why touching the owls is uncomfortable for the bird. The birds instinctively regard humans as predators. Since predators would not normally touch or pet their prey other than trying to kill it, a wild bird's natural reaction is to avoid being touched or to defend itself when approached.

Ms. Wiebe touched on cosmetics of education birds. MWRO tries to accurately represent the birds as they appear in the wild, avoiding disfiguring disabilities, such as severe head injuries or amputations. This helps inspire respect for the natural beauty of the bird instead of pity. When people ask about keeping the owls as pets, she gets into quality of life issues for the bird. She talks about their specialized diets, housing requirements, and how difficult it is to secure a steady supply of rats or mice, adding these items are not readily available at the local pet shop. She uses the example of how a Great Horned Owl can sink its talons through a hand without even blinking to illustrate how dangerous some birds can be, pointing out the heavy gloves required when handling the owl.

Ms. Wilson opened the discussion up to the audience for comments or questions.

Randy Love, Alberta Educational Association: Mr. Love's experience at the Calgary Zoo using amputee owls in educational programs is that often times people don't notice the bird's injury. Ms. Wilson concurred, and when she has her students guess the bird's disability, her own Eastern Screech-owl's amputation goes unnoticed until the bird flaps its wing.

Lorraine Andrusiak, (Ms. Andrusiak), researcher, ecological consultant and associated with a British Columbia wildlife rehabilitation organization: In British Columbia, releaseable and physically deformed owls are not allowed to be used in educational programs or displays.

Ms. Wilson: The panel was asked to reflect briefly on how the regulations vary from province to province and in the U.S.

Ms. Wiebe: In Manitoba, since there is really only one organization doing rehabilitation, regulations are in the process of being formulated, for which MWRO strives to set the standard now in the early stages.

Ms. Wilson: "During many of my programs, there's always a kid who asks, 'When are you going to let the owl fly around the room?' My U.S. state and federal permits do not allow that. The owl could potentially hurt itself or an audience member." Ms. Wilson next asked the panelists to touch on the question of liability when using live birds close to people.

Mr. N. Smith: He said, no, he does not let his birds fly around and explained that his facility, owned by the Massachusetts (state) District Commission and operated by the (private, non-profit) Massachusetts Audubon Society, is in fact required to carry $10 million in liability insurance coverage because of the potential risk of injury. Mr. N. Smith noted that Massachusetts has a history of high monetary claims. Since facilities don't "own" their non-releaseable wildlife, the fate of non-releaseable birds rests with the state's director of non-game species. His office determines where various individual non-releaseable birds are placed. For example, an endangered Peregrine Falcon is more likely to go to a facility such as Blue Hills' that reaches 400,000 visitors per year and has the liability coverage than a smaller operation that reaches several hundred people. Mr. N. Smith doesn't let visitors get too close to the animals. He added, "Liability certainly is an issue we think about all the time, and something I never thought about in the past until we started paying these insurance premiums. Now we think about it all the time."

Ms. Wilson: "Well, thanks to you, Norman, now we're paying insurance premiums, too!" Ms. Wilson motioned to the crowd of people, including several children, standing in the doorway to please come in.

Dr. Bob Nero: "I haven't heard much about the preparatory work yet, and Rick (Smith) will vouch for this. I require the class, or the entire school, to study owls in considerable depth. By and large, I practically demand that all the people in the school have the opportunity to see one or more educational films, slide sets or whatever, on Great Gray Owls, because that happens to be my particular topic. Invariably, they study owls of many different kinds." For the half minute, the Great Horned Owl has been preening on its perch, and now rouses its feathers with a great shake. More eyes are on the owl than Dr. Bob. "I can't compete with that bird!" he huffs lightheartedly. "The second requirement for my program is the kids have to become involved, to the extent that's feasible and permissible, in fund raising in support of endangered species. The owl (Lady Grayl, Dr. Nero's tame Great Gray Owl) and I come to the school as a reward for the hard work that the students *and* teachers have done. I think that makes our presentation that much more effective."

Dr. Nero offered two examples to illustrate the extent to which this works. "At an inner city school here in Winnipeg, as I walked into the school with the tame Great Gray Owl on my glove, with the kids in the hallways leaning back against the wall saying, 'Gosh! It's alive!', I heard a grade 5 Vietnamese boy point to the owl as we went by and say, 'Nictitating membrane!'. I thought, 'This is going to work.' One more example: In a grade 4 class, each student had studied a different species of owl. One student asked, 'Could you tell me please the clutch size for Blakiston's Fish-owl (*Ketupa blakistoni*)?' I said, 'Sure! If you can tell me the scientific name.' The kid knew it!"

Ms. Wilson: "Well, that's a great lead in to talk about the preparation that the kids do with the teachers. Many of the teachers are also doing research." Ms. Wilson mentioned the teacher's kit she sends to the head teacher once a program is booked that consists of a list of owl books, videos and audio tapes, a source for owl pellets and field trip ideas to see owls in captivity and where to look for them in the wild. Teachers can work the information into their curriculum and become more knowledgeable themselves. She asked Mr. R. Smith to reflect on some of the preparatory work that he does with his students before a visit from the "Grand Master" (Dr. Nero).

Mr. R. Smith: "In this day and age, with the spending cuts in schools, it's very difficult sometimes to get the resources we need. I try to do my homework. Between September, when I first contacted Dr. Nero about an owl program, and March, when we finally met, Dr. Bob had lots of resources for me and lots of time. We were able to show some videos to all the students in the school. I don't want to just bring an owl in and it's just a one shot deal. I want to make some real life connections and some connections in curriculum." Mr. R. Smith worked closely with the school's computer teacher, set up a research project where the students studied a particular owl, and focused on owls in Canada, especially the endangered ones. He found this tied in well at the grades 4-5-6 level, beginning with study of habitats, and on to adaptations, wild communities and populations, environmental awareness, reclamation projects, sustainable develeopment, and so on.

Ms. Wilson: "Think about what you were learning in sixth grade. Were you doing it at that level? I know I wasn't." Ms. Wilson said teachers are using owl study in their curriculum at a pretty complex level. Students are eager to study a particular owl species on their own. She next moved to discuss use of owl pellets in the classroom to illustrate food chains and the web of life. Middle school students get hooked on studying owl pellets. She asked the panel to reflect on their use of owl pellets, sources of owl pellets, and whether they use pellets from their own research.

Mr. N. Smith: "During my Snowy Owl project, my two assistants collected over 5,000 pellets. We've utilized some of these pellets in school programs and have kids take them apart, and have them try to analyze what the owl has eaten." Mr. N. Smith recalled a rainy day when his son had a friend visit. His 4-year-old son asked his friend, "How many pellets do you have in your collection?" Because his son had grown up with this, he assumed that everyone in the world had a pellet collection. While the pellets collected from wild birds were better than those from his captive birds, it made no difference to the student dissecting a pellet, hunting for the prized skull it contained.

Mr. N. Smith described an inner city class that came to his museum as a follow-up after a live owl program and session of pellet dissection. "As the children got off the bus, they were screened for weapons. These kids are real tough kids. By the time those kids left at the end of the day, those kids were the friendliest kids we'd ever met, and they said, 'when can we come back?' The only things they have at home are drugs, fights on the streets, and nothing fun or exciting to do. These kids were thrilled to get an opportunity to have a day to come out exploring and dissect a pellet. So it can actually change somebody's life—a little, old, regurgitated pellet."

Ms. Duffy: "The pellets I've used are either ones I've collected myself or have come from rehabilitators I know. Sometimes I pass around a bag with a pellet in it. That way, I can reuse it. I teach them how to search for pellets on their own."

Ms. Wilson: "We're constantly encouraging the kids to look for owl sign as clues to owls' presence. We use the pellets as one of those clues as well as learning about whitewash and owls' calls to teach them how to observe owls without disturbing them. So, the pellet really works into all different levels of owl study." Ms. Wilson next asked the panel and attendees to discuss the sources for owl pellet, stating that teachers can order large quantities of owl pellets from large biological supply houses, paying a few dollars per pellet. Where do these pellets come from and how are they collected? She's been approached over the years by researchers and educators concerned about possible impacts on wild owl populations, particularly during the nesting season.

Mr. R. Smith: He was anxious to use owl pellets as an educational tool, and his first instinct was that if pellets were being sold commercially by big supply houses and had been fumigated as advertised, they must be legitimate. Then, after Dr. Bob Nero mentioned possible disturbance factors and instead offered some of Lady Grayl's pellets, Mr. Smith approached his administrator with the idea. They found they'd stepped into a gray area of questions about possible health risks like allergy and sanitation concerns with bringing unfumigated owl pellets into the classroom, creating a dilemma. At this time, in the city of Winnipeg and across Canada, he explained, elementary schools can no longer dissect dead animals. Realizing they were entering uncharted territory and were concerned about buying from a big company, unfortunately they opted not to do it. They thought about sending home a parental consent letter, but, Mr. R. Smith concluded, "Do you want to get into that political hotbed of having that all happen? We live in a fairly volatile community and wouldn't want anything to happen. It wouldn't take long for some people to bring charges. He realized he was breaking a bit of ground as a grade 6 teacher. "All of a sudden, you're saying, 'Whoa! I don't need all this extra hassle'. All I wanted to do was dissect some owl pellets and have the kids learn a little bit more, so in the end, we opted out of it. I kind of feel my kids got cheated out of a valuable learning experience because there didn't seem to be any clear-cut school policy on it. Hopefully, next time we can go in a bit more educated about it."

Ms. Wilson: Ms. Wilson allowed that there were many unanswered and perhaps unanswerable questions about health hazards to students and disturbance problems to wild owl populations.

Ms. Wiebe: "The kids claim that they are Barn Owl (*Tyto alba*) pellets."

Ms. Wilson: Her understanding is that most are Barn Owl pellets that have been fumigated. The only company that she currently recommends in her teacher's kit is a small operation on the west coast on which she had gotten a good recommendation from an owl researcher.

Pat LeClaire (Ms. LeClaire), school teacher, Winnipeg: "I'm here with Dolly Chisick, we're disciples of Dr. Nero, and we've been honored with having him visit 2 years during my 9 years here. We've used pellets successfully and get them from Pellets, Incorporated in Washington. They are perfectly healthy. The kids come with rubber gloves, but by the end of the hour, the gloves are off, and they are just so involved in it. I can just see their participation and excitement. It is *the* hot topic in grade 5 and has grown in reputation at our school."

Ms. Wilson: "Yes, and it's the disgusting aspect of it that makes it all that much more attractive to these kids. We need to think of the tradeoffs coming into play here."

Ms. Andrusiak: Ms. Andrusiak conducts Barn Owl research and has run into numerous problems with pellet collectors. For instance, she had an opportunity to band Barn Owls at a nest study site, located on a private farm. When she arrived to ask if the owners would allow her to band the owlets, she was abruptly told, "I'm sorry, but this guy comes up from Washington to collect pellets and has asked us to not let any other owl people in with the owls." So, she was not allowed in to band the owls, posing a problem for her work. She said the barn owners seemed happy that this man comes, he tells them they're for educational purposes, and don't realize that he's selling them. As far as she knew, the property owners do not get a financial cut from the operation, but Ms. Andrusiak's main concern was that the birds were being disturbed.

Ms. Wilson: Ms. Wilson added concerns she had heard from East Coast researchers about Barn Owl populations being disturbed by pellet collectors, and admitted that there were no clear cut answers yet to this conflict. Ideally the activity should not be conflicting with research or annual nesting and/or roosting cycles of any owl species. She suggested pellets might be collected from former roost sites after the birds have gone.

Michelle Kading (Ms. Kading), Director of Interpretive Programs, Oak Hammock Marsh Interpretive Center, north of Winnipeg: About 1,300 children visited Ms. Kading's facility in 1996 and participated in owl pellet dissection, with 3-4 students per pellet. She purchases fumigated pellets from Pellets, Inc. in Washington. "We're probably one of the bigger pellet consumers in the province." She also buys pellets from Educom in Toronto, but they sometimes have trouble keeping up with Oak Hammock's demand. She, too, was concerned with health issues, and called the companies and made sure the pellets were fumigated. "They're not as expensive as you might think, about $2.25 per pellet, and come wrapped in foil. The kids call them 'baked potatoes.'" Last year, Ms. Kading got a call from a public health nurse because a school child was about to come dissect pellets, and the parent was concerned about pellets transmitting the Hanta virus. The mother knew the virus was found in mice, that owls eat mice, her child was going to touch the owl pellet, and was afraid the child would get Hanta virus. Both companies confirmed to Ms. Kading that Hanta is contained in the blood system and with fumigated pellets there was no danger.

Ms. Wilson: She clarified that fumigating pellets means they've been heated, or autoclaved, at high enough temperatures to kill any bacteria or virus, and presumably make them safe to handle with usual safety precautions.

Ms. Kading: "We strongly suggest that people do not collect their own pellets, because an untrained person, or, even one of my own staff who was very keen on owl pellets, came back with what he thought were real owl pellets that were in fact coyote droppings. Both handling coyote droppings and inhaling near wolf droppings can be very harmful to people." She feels it's very dangerous if you don't know what you're looking for, except for a trained expert.

Ms. Wilson: "Here's an example where the school groups are coming to you, and you can suggest that the teachers and students do their preparatory work beforehand to learn the differences in size, shape, and composition between owl pellets and animal scats or feces. There is a fine line there where you still may not want the kids to be picking up owl pellets on their own, but just use them in the wild as a sign that owls are present."

Rick Gerhardt, Oregon: "The Centers for Disease Control (CDC) in Atlanta (Georgia) has a disease control packet available free specifically addressing Hanta virus. Also, I do have one aquaintance making his living in Oregon collecting pellets, selling them to Carolina Biological Supply which pays him $.50 per pellet. He spends most of his time driving around collecting Barn Owl pellets." Mr. Gerhardt said collecting does not have to be an invasive activity if done in the right season, and this aquaintance seemed sensitive to disturbance, adding it's not a goldmine, either. He thought he might be making $20,000 per year, but it's a full-time job.

Mr. Chester, Medicine Hat: Mr. Chester operates a nature store that sells pellets and has one partially dissected on display. His supplier is Edu-fund in New York. Some pellets are bought by schools, but many are bought by adults with children, and he finds the adults are often more interested than the kids. He is in the position of teaching the adults at the counter about owls and the food chain, and he feels there is a real need to increase educational programs directed toward adults, too.

Ms. Wilson: "Oh, yes! The adults are fair game. We do lots of adult programs."

Ms. Kading: Oak Hammock Marsh got a request to buy owl pellets from the Rockwood Institute, a correctional facility, next to Stony Mountain penitentary. They thought this would be a wonderful thing to do with their adult residents.

Dr. Nero: "Good use of pellets for jailbirds!"

Ken Bevis (Mr. Bevis), formerly with the U.S. Forest Service contributing to the CDC's research into Hanta virus, Washington: "The Hanta virus is a very fragile virus. It has a lipid coat and they don't think it really has a very long life span outside the actual fecal matter or urine of the actual rodents themselves. So, it's unlikely, at least from what I've read, that the virus would be transmitted through a pellet due to time and probably the digestive action of the bird. As an aside, we've been doing a whale of an experiment with everybody handling pellets, so if it was a problem, we'd probably know by now!"

Ms. LeClaire: "It hasn't bothered me for 9 years. I'm still here."

Mr. Bevis: Ms. Wilson confirmed with him that the Hanta virus is transmitted through the feces and the urine, rather than through the digestive system of the owl. Mr. Bevis added, "From what I've read, CDC really doesn't know, because it's a rather mysterious virus, but it's probably not a problem in pellets. That's the feeling that I got."

Ms. Wilson: "Now, Dr. Bob (Nero), maybe you'd reflect on how pellets taste. I know you've tasted pellets. You didn't get sick from that, did you?" she asked lightheartedly.

Dr. Nero: "No, the mucus coating is sweet. The interior is rather unpleasant."

Ms. Wilson: "But you're here to tell the story! This is some great information and it makes me want to encourage a general awareness of how you, as researchers, if you're out collecting pellets, can recycle them. I mean if you have trash barrels full of them, perhaps if after you're done getting weights and analyzing them, etc., if they're intact, rather than just disposing of them, autoclave them to take care of the sanitation problems and donate them to some local schools for educational use. They really *are the nut* in using owls in education and getting kids to really think about the whole food chain, and boy, it's just like a little prize when they pull that skull out! It's a real game for them." Ms. Wilson went on to tell of a photo sequence in her program showing a Great Gray Owl coughing up an owl pellet. The last slide shows the pellet in the bird's bill. Using the sequence, she teaches the students how to "hock up an owl pellet." At the prodding of the audience, she proceeded to go through the motions, with some animation, while explaining the process. "With the final slide, I tell them the pellet is still steaming by the time I pick it up and pull the skull out of it. So, we really get the kids excited and they love it."

Ms. Wilson gave a brief overview of how owls are transported to and from programs. Some owls, like Lady Grayl, travel on perches. Others, such as her own, travel in ventilated, wood carriers with astroturf perches and removable astroturf floor mats. Ms. Wilson sets up a fan behind the boxes for added circulation. Mr. William Dove, a British Columbia educator, travels with his owls and other raptors on the road for a month at a time across the province. "Obviously, people such as ourselves who care about owls as much as we do make sure the owls are as comfortable as possible on the road. We get the kids to thinking about how the birds can overheat and become dehydrated in hot, dry buildings, and often cool down the room ahead of time. But, everyone always wants to know, 'Do they live in this box all of the time?'" She asked Ms. Wiebe to hold up the Great Horned Owl's carrier.

Ms. Wiebe: She explained this new type of soft-sided, lightweight traveling box that MWRO is trying. It has a wood frame, and a nylon, breathable, removeable cover that stays dark inside, yet goes into the washing machine.

Ms. Wilson: "Let's end up with owls on line and a discussion about how information is being dispersed and how all of us can communicate a little better. Clearly, one reason we educators, and some of us are researchers as well, are here at this symposium is to recharge our batteries, gather information as fodder for our programs, and keep abreast of research work that's being done on different species or various aspects of owl biology. Our challenge is to interpret this information into terms that can be understood by different age groups. How is the Internet being used to disperse information both to you on the panel and to kids in the classroom? Do you have your own home page, Norman?"

Mr. N. Smith: Although Massachusetts Audubon does have a home page, he confessed he is not a computer person. His staff takes care of it. "To be honest with you, right now, I'm just looking at these figures here. I figure with 5,000 pellets at $2 per pellet, I owe my assistants about $10,000!"

Ms. Wiebe: "We are on line at the center (MWRO) through member's home computers. I get downloaded articles dropped off to me written by other rehabers. I can also have my own questions posted on the computer bulletin boards and get responses back fairly quickly, so it's working really well with us."

Ms. Wilson: "Rick, how do you get those kids away from their computer screens?"

Mr. R. Smith: "We're really fortunate to have a computer library with 18 computers available to the students. I work closely with my computer librarian, my best friend, and she bookmarks anything relating to the projects she knows I'm working on. The Internet is really big with kids."

Ms. Wilson: "So, what I want to know is, do the kids take it to the next step? Does it get them out observing wildlife outdoors, or do they search more in the real world? I know a lot of us as educators are concerned that kids are growing up with a perception of wildlife as viewed on a TV screen or computer monitor, and not actually experiencing the hooting of a Great Horned Owl in the wild, or the magic of a Great Gray Owl hunting, or a Hawk Owl plunge-diving, or some of the things that really excite all of us as birders and researchers—the stuff that all of us see.

Mr. R. Smith: As a pretty progressive, small school, he feels fortunate to be able to involve his students in some field research projects. Last year, a fellow teacher involved students with Fort Whyte Environmental Education Center and studied Canada Geese migration and staging behavior. This is an 8-week hands-on program. He wants to involve his grade 6 students more in outdoor experiences, and has written a grant proposal for $20,000 to involve them in a sustainable development project. If the grant comes through, they plan to develop a CD-ROM which could be shared with other schools.

Ms. Duffy: As an interpretive naturalist, Ms. Duffy, while computer literate, believes virtual reality can't match real reality. When asked if the children who go out on her nature walks at Grand Teton National Park in Wyoming recognize wildlife and know something about it already, she responded, "I live in Wyoming where there are Bald Eagles and coyotes and Great Gray Owls and all kinds of amazing wildlife. I ask the kids, 'Do you realize how lucky you are because of where you live? Other kids only see this on television.' One third grader said, 'Yes, my parents remind me every day!' I try to show them that the Internet is a tool they can use to learn about wildlife."

Ms. Wilson: "So, you can just feel her level of excitement. It's as if she has a kids' group right here with her, but that's how educators who are also researchers or are aware of research can get excited with kids and adults and make them want to get out and experience what's left on this planet."

Ms. Scottie Dayton (Ms. Dayton), Editor, Owls Magazine: Ms. Dayton told of a Microsoft commercial that was supposed to be run during the Superbowl depicting a whimsical scene of a girl clutching an injured Great Horned Owl. The father explains she doesn't know anything about how to help it, but she goes to her CD-ROM and learns how to treat it herself in her home. The ad ends with a scene of a healthy owl. The ad gave inaccurate information and made no mention of professional rehabilitation facilities.

Mr. Don Middleton (Mr. Middleton), Educator, MWRO: Mr. Middleton said there are about 850 rehabers that talk through e-mail. Due to objections to the ad by rehabilitators and their ability to mount a massive campaign to remove the ad using the Internet, the ad was not shown during the Superbowl. "The Internet has the potential to mobilize researchers and those who care about wildlife in a way that we never could before. There was mention of people who grow up never seeing a tree. Those people can still care. The way that we're going to educate people is going to be through every device that we have."

Ms. Dayton: "Tuesday, the commercial Microsoft ran in its original form again."

Mr. Middleton: "So, we need to go back again."

Mr. Tom Sprout, raptor researcher and educator, Ohio: Mr. Sprout attributed his work with raptor rehabilitation and research to the interest that certain people took in educating him about wildlife at a very young age. He stressed the need to integrate education and research more at a grassroots level. He often involves the whole community in a project. "They won't preserve it, they won't save it, if they don't understand it. A lot of the researchers I know say, 'I don't have time to bring lay people into my research. These same researchers won't give me money to do my research and these grants are getting cut. The public won't support our research if the public isn't aware of

what we do." Mr. Sprout added a success story where two churches donated time, labor and lumber to build nest boxes for his research. He now has 30 new boxes with which to begin his spring research because the young people came and experienced the Barred Owls in his research project.

Ms. Wilson: "And you got them all the visibility in the community, a lot of goodwill, and you got your boxes. So, everyone comes out a winner on that one!"

Mr. Brian Linkhart, Flammulated Owl biologist and high school teacher, Colorado: Mr. Linkhart uses his research, owl pellets, and hands-on activities to turn kids on to the natural world and science. "It's an opportunity that kids never forget. We all see the world through our experiences. These kids have had profound environmentally oriented impacts made upon them by experiences in the field."

Ms. Wilson: "I'm sure a lot of you can sympathize with the extra effort it takes to take a group of kids out or that extra mile that you do have to go to have the patience with both children and adults, and the development of your own interpretive communication skills in order to teach about a subject that *you* know so well, but that they really know nothing about. So, it is really worth going that extra mile."

Ms. Duffy: Ms. Duffy offered a handout she had prepared, "Involving the Public—Tips for Researchers", that provides researchers with ways to integrate education into their work. "Think about what's in it for you. Do involve the public. You'll love it, too!"

Ms. Wilson concluded the workshop by reading a passage from Dr. Nero's book, Lady Grayl (Nero 1994). Speaking to the mysteries of owls, she sets the scene—"It is 5 January 1989, midnight,—12°C; Dr. Nero is in the owl's outdoor pen and the owl is facing southeast very intently"—and reads:

> "When she turns around, finally, she looks at me only briefly, large pupils giving her a gentle, benign look. But my poking and prying bother her little and she keeps looking around, at times swinging her head suddenly as if a sharp noise compelled her. When the dog, running happily loose in the snow in the night, comes running by, she turns and looks down at him, but without any alarm, then returns to her vigil. I am awed by her attentiveness, puzzled by the forces that drive her, impressed by her seeming spirit of wildness. Is this what the wild owls are doing at this very moment, I wonder? Perhaps the well-fed ones? I should stay out here all night to record what she does, but I'm tired, so I call the dog and go off to bed."
>
> When I return in the morning at 7:15 AM, she is sitting in the same place, facing the same direction, apparently still doing the same thing. I am stunned by the awesome thought that this bird can do this through the night. What incredible attentiveness. She is never bored. Every little movement, each little sound, patterns of branches against the night sky, the sound of the wind, these realities and presumably many others beyond our scope excite and interest her."
>
> When I think of the long-distance movements of some of our radio-marked owls, as much as 800 km in less than 3 months, I think that these birds have capacities we are just beginning to glimpse. And this tame bird, no less, still has inherited patterns of response, feels things, has inner compulsions. I am witness to a spirit. I realize what little there is beneath this feathered form—a small body, long legs, not a great deal of mass, the brain—no, what we have here is the spirit."

In closing, Ms. Wilson asked Ms. Braun to walk with the live Great Horned Owl down the center aisle of the room, giving the audience a chance to see the owl up close, ask questions, and to ponder the yet undiscovered mysteries of owls. Just as this beautiful, pale Great Horned Owl starts down the aisle, she hoots, delighting all present, and leaving her own mark on this inspiring workshop.

ACKNOWLEDGEMENTS

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LITERATURE CITED

Cruickshank, H. 1964. Thoreau on birds. New York, NY: McGraw-Hill Book Co. 331 p.

Nero, R.W. 1994. Lady Grayl.: owl with a mission Toronto, Ontario. Natural Heritage Books. 176 p.

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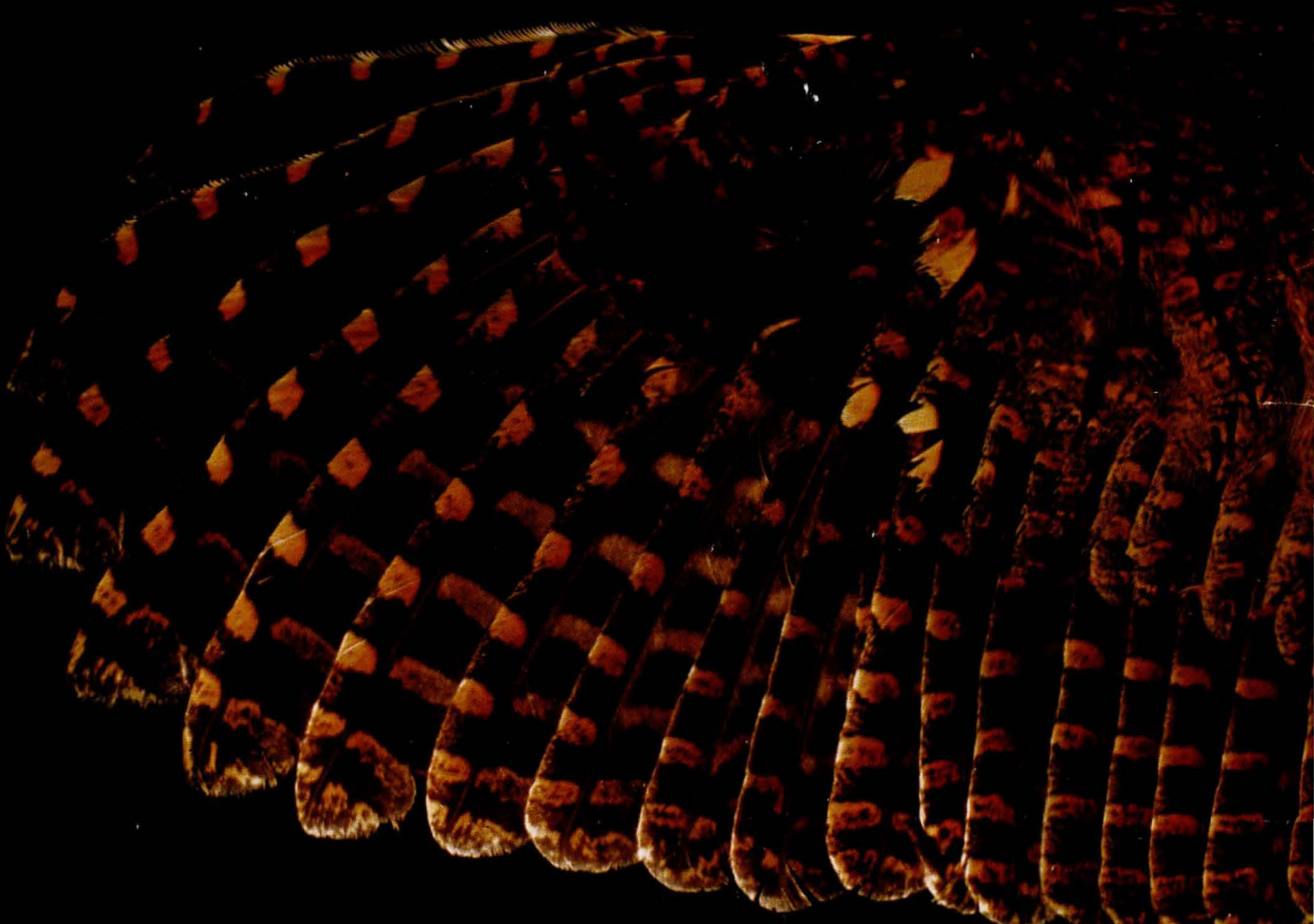
The Proceedings contains 91 papers authored by 143 people from 13 countries covering biology, ecology, monitoring, habitat-use, status, conservation, education, genetics, toxicology, diet, migration, mortality and related topics concerning owls of the Northern Hemisphere. Thirty-three owl species are discussed. Information presented will be useful in owl conservation, management, identifying research needs and defining conservation priorities.

KEY WORDS: Birds of prey, raptors, predators, prey, birds, feathers, habitat, snags, nests, wildlife conservation, owl ecology, wildlife management, bird migration, radio-telemetry, habitat modelling, population monitoring, surveys, geographical information systems.

Our job at the North Central Forest Experiment Station is discovering and creating new knowledge and technology in the field of natural resources and conveying this information to the people who can use it. As a new generation of forests emerges in our region, managers are confronted with two unique challenges: (1) Dealing with the great diversity in composition, quality, and ownership of the forests, and (2) Reconciling the conflicting demands of the people who use them. Helping the forest manager meet these challenges while protecting the environment is what research at North Central is all about.

NORTH CENTRAL
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